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POHLIA HEDW. (MUSCI) IN NORTH AND CENTRAL AMERICA AND THE WEST INDIES

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Within the Bryaceae, basic features defining *Pohlia* are lanceolate, often serrate leaves, costae ending before or in the apex, and long, generally narrow cells. The peristome is double and the endostome is well-developed although cilia, when present, generally lack appendicula. Groups of taxa within the genus are more or less uniform with respect to such attributes as exostome and endostome form and ornamentation, exothecial cell shape, the presence or absence of annuli and the position of stomates relative to their guard cells. Within such groups, species differ mainly with respect to gametophytic details. Axillary gemmae have evolved at least twice in unrelated lines. Rhizoidal tubers are present in *P. lescuriana, P. pacifica* and *P. integra*, and are of some use in characterizing these species.

The group of species segregated by some as the genus *Mniobryum* are included here in *Pohlia,* although it is fully acknowledged that *Mniobryum* constitutes a distinctive assemblage. The presence of such species as *P. lescuriana*, which is a *Pohlia* by any definition but approaches the *Mniobryum* group in several significant respects, makes including the latter as an infra-generic taxon in *Pohlia* at least defensible. Crum and Anderson (1981), following Andrews (1935), placed *Bryum apiculatum* Schwaegr. (= *P. cruegeri* Hampe *ex* C. Müll.) in *Pohlia*. However, I agree with Ochi (e.g. 1981) that it is more at home in *Bryum.* It is the long cells that might indicate a relationship to *Pohlia*, but this trait is to be found rather frequently elsewhere in *Bryum.* In addition, the costa is shortly excurrent, and the leaf margins are entire (or vaguely serrulate), features uncommon in *Pohlia.* Although appendiculate cilia are found in a few *Pohlia* species, they are uncommon, and their presence in *B. apiculatum* casts further doubt on a closer relationship to *Pohlia* than to *Bryum.* Finally, the lowland circumtropical distribution of *B. apiculatum* would be unique in *Pohlia,* though not rare in *Bryum. Pohlia peracuminata* Bartr. from Guatemala is a similar case where generic placement is uncertain, but according to Ochi (*in litt.* 1981) it can be referred to *Bryum microchaeton* Hampe.

I also follow Ochi in interpreting *Anomobryum* as more allied to *Bryum* than *Pohlia*, although generic status seems justified. The long-narrow cells, which are not even characteristic of all *Anomobryum* species, is the only feature that relates *Anomobryum* to *Pohlia.*

With about 110 species, *Pohlia* is represented on every continent. The circumboreal taxa are by far the best understood, and of the thirty-two Pohlias in North America north of Mexico, twenty-five occur on at least one other northern continent. There have been no revisions of tropical or Southern Hemisphere species.

Many of the American *Pohlia* species are rare throughout their range and the genus is poorly represented in temperate eastern North America. *Pohlia melanodon* and *P. lescuriana* are restricted to eastern North America and are fairly

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widespread, though relatively uncommon (*P. lescuriana* is also known from two localities in Alaska). *Pohlia wahlenbergii* and *P. nutans* are common in the northeastern states and extend southward to a considerable extent. Otherwise, species reaching Tennessee and North Carolina do so by following the Appalachian mountain chain. These include *P. cruda, P. elongata,* and *P. longicollis. Pohlia annotina* is fairly widespread in eastern North America, in the mountains and elsewhere.

In the Rocky Mountains and westward, *Pohlia* is one of the most diversified of moss genera. Collecting on the slopes of Mt. Rainier (Washington) for example, can yield up to eight species in a day. Relatively moist areas with acidic soils in the mountains of southern British Columbia are also uncommonly diverse in *Pohlia* species. Several species extend southward in the Rockies to Colorado, but only *P. elongata, P. nutans, P. wahlenbergii* and *P. tundrae* are confirmed in Arizona and (or) New Mexico.

Of the North American species, *P. elongata, P. cruda, P. nutans* and *P. wahlenbergii* reach Mexico, but only *P. elongata* is common there. Other species of Mexico and Central America are either endemic, for example, *P. integra, P. oerstediana* and *P. pseudo-barbula*, or have phytogeographic affinities with Andean plants. The latter includes *P. richardsii* and *P. polycarpa.*

Of the *Pohlia* taxa occurring north of Mexico, six (19%) are endemic. Three of these are found in the Pacific coastal region near or at sea level (*P. longibracteata, P. columbica* and *P. pacifica*), whereas the other three are alpine-high montane in the Cascade and (or) Rocky Mountains. Endemism in Mexico and Central America is more difficult to evaluate since collecting there has been relatively scarce. *Pohlia integra* and *P. pseudo-barbula* are confined to mountains near Mexico City, and *P. oerstediana* extends from central Mexico to Costa Rica. There are no West Indian *Pohlia* endemics and only *P. elongata, P. wahlenbergii, P. richardsii* and *P. papillosa* are known from the islands.

As a whole, *Pohlia* covers a significant diversity of habitats. Most taxa occur on soil, although the substrates of particular species are usually well-defined in terms of pH, texture, organic matter content, and the levels of various ions. The *Mniobryum* group (species 29–36) is found almost exclusively on soils of high pH, 6.5 or above, and low organic content (less than 2.5%). Of those species only *P. longibracteata* occurs frequently on more acidic soil. Species 14–17, including the group of weedy propaguliferous species, also prefer soil with relatively low levels of organic matter (3.5% or less), but they usually occur on mildly acidic soil. The remaining species are almost entirely restricted to acidic soils (pH 4–6).

By far the most common habitat in which to find Pohlias are roadbanks and other disturbed sites. Some such species as *P. annotina* are rarely collected in undisturbed habitats, although most other, less weedy species are found also on streambanks or in soil-filled crevices. Several species reach the alpine zone, and *P. crudoides, P. longicollis* and *P. andrewsii* are characteristic of crevices among siliceous rocks in tundra. Most other species, when they occur in the alpine zone, grow in more exposed sites. *Pohlia obtusifolia* and *P. bolanderi* var. *seriata* prefer exceptionally lush snowmelt areas. *Pohlia sphagnicola* is unique in being restricted to *Sphagnum* hummocks lacking mineral soil.

The main purpose of this paper is to provide an aid in identification. The infra-generic evolution and classification of *Pohlia* will be dealt with elsewhere, and the genus is left undivided here. However, the arrangement of species is intended to represent relationships, insofar as a linear sequence can. Species 1–13 have long-rectangular, nonsinuose exothecial cells, whereas in species 14–35 they are short-rectangular to isodiametric, usually with strongly sinuose walls. Species 10–13 have whitish exostome teeth densely covered with papillae (less so in *P. pseudo-barbula*) and lack cilia altogether. I have dispensed with tradition in, for example, placing *P. elongata* next to *P. nutans* rather than with other species having narrowly split endostome segments. It is open to question whether endostome simplification has occurred only once in those species, and the present arrangement is intended as noncommital, reflecting gametophytic as well as sporophytic similarity. Of the species with sinuose exothecial cells, 14–27 have annuli, while they are lacking in 28–34. In species with sinuose exothecial cells, they become nearly straight when thoroughly moistened. Axillary gemmae characterize species 11–13 and 17–26.

Many problems relating to nomenclature and typification are not discussed for the sake of brevity. The location of lectotypes are indicated, and further details on specimens are available from the author. The problem of *in* versus *ex* in some author citations was not resolved completely. In such cases as *Webera columbica* Kindb. *in* Kindb. & Macoun, the *in* allows the name to be typified from Kindberg's herbarium, as most bryologists would agree it should. It should be admitted that in such other cases as *P. longibracteata* Broth. *in* Roell., the choice of *in* is to facilitate typification since there is little evidence from the original publication to make a decision as to whether *in* or *ex* is more appropriate.

A revision of species 18–26 was published previously (Shaw, 1981a), and only brief descriptions and illustrations are given here. *Pohlia beringiensis* (17) is described for the first time. Although sterile, similarities in gemmae structure relate it to *P. drummondii* (18). Gemmae similar to those of species 17–26 are produced by *P. papillosa, P. richardsii* and *P. pseudo-barbula*, but other characters, especially sporophytic, indicate that the two groups are only distantly related.

Keys are provided for both fertile and non-fruiting plants, although identification may require at least a determination of sexuality. The key to non-fruiting plants is offered somewhat apologetically since gametophytic distinctions, though often reliable, are difficult to define and consequently to use.

Except where noted, geographic distributions given are based on specimens examined. I did not attempt to exhaustively document the local distributions of such common species as *P. wahlenbergii, P. cruda* and *P. nutans*, and so maps should be considered synoptic. Greenland distributions shown on maps are given incidentally.

Pohlia Hedw., Spec. Musc. 171. 1801.

Webera Hedw., Spec. Musc. 168. 1801 (hom. illeg., non Webera Schreb.).

Lamprophyllum Lindb., Oefv. K. Vet. Ak. Foerh. 20: 12. 1863 (*hom. illeg., non Lamprophyllum* Miers.).

Mniobryum Schimp. *ex* Limpr., Laubm. Deutsch. 2: 272. 1892.

Small to robust, glossy or dull plants generally forming populations of restricted size, occasionally mixed with other mosses. Stems erect, short to very long, simple or branching at the base or less commonly above when sterile, simple or often innovating when bearing gametangia, in transverse section round to pentagonal, with a ± distinct central cylinder of small, thin-walled cells, 4–7 rows of gradually larger thin- to thick-walled cells and 1–4 (–6) rows of small, often pigmented thick-walled peripheral cells. Rhizoids pale orange-red to brown, papillose, sometimes bearing tubers. Leaves little altered when dry, symmetric or ± asymmetric, lanceolate to ovate-lanceolate (linear in the S. Hemisphere *P. tenuifolia*), acute or rarely rounded at the apex, generally ± decurent; margins plane to recurved (especially the perichaetial bracts), serrate to serrulate or rarely entire near the apices, entire to serrulate below; costa single, ending above mid-leaf to percurrent, rarely shortly excurrent, occasionally abruptly widened below, in transverse section rounded to plane on the ventral (upper) surface, ± strongly convex on the dorsal surface, with 2–4 median guide cells, a ± well-developed dorsal stereid band, sometimes a few ventral stereids, and 1 row of enlarged firm-walled cells on the dorsal and ventral surfaces; upper cells hexagonal to linear, sometimes large and lax, smooth, with thin to thickened walls, lower cells hexagonal, often quadrate across the insertion, marginal cells undifferentiated or in some species longer and narrower than the median. Propagula sometimes present in the upper leaf axils, arising singly or in clusters of 3-many, consisting of a multicellular body and (0–)1–4 apical or subapical leaf primordia. Dioicous, paroicous or rarely autoicous; perichaetia terminating short to elongate main stems, the bracts scarcely to strongly differentiated, with recurved margins; perigonia terminal on main stems or sometimes innovations, the bracts shortly acute to longly acuminate from an ovate, concave, ± red-brown base, erect to spreading or sometimes squarrose from the erect base; paraphyses filiform, orange to pink. Sporophytes rare to common; setae erect, in transverse section similar to the stem but with a more strongly developed central cylinder; capsules 1 or rarely more per inflorescence, inclined to erect, ovate-pyriform to linear-cylindric, sometimes urceolate, with a well-developed neck, very small to large; exothecial cells isodiametric to elongate and rectangular, sometimes collenchymatous, the walls straight to sinuose, smaller, thicker-walled and less sinuose near the rim, isodiametric with thin to firm, straight walls in the neck, gradually more elongate with thickened, straight walls just above the seta; stomata abundant in the neck, with 2 guard cells, superficial, sunken, or deeply immersed; annuli well developed to absent, (1–)2–3 rows of cells, revoluble or separating irregularly; opercula conic to convex, acute, apiculate, umbonate or rarely rostrate; calyptrae cucullate, smooth; peristome, double; exostome teeth 16, lanceolate, acute to acuminate and 300–550 μm long, or rarely ± blunt and about 150–300 μm long, strongly to obscurely bordered, with dorsal plates wider but ventral plates thicker; endostome well-developed or incomplete, hyaline or sometimes yellow; basal membrane low to high; segments generally elongate and keeled, broadly to narrowly (or not at all) perforate; cilia long and nodulose to short or absent. Spores very finely to coarsely roughened.

KEY TO STERILE PLANTS

1. Plants bearing axillary gemmae.
  2. Gemmae arising singly in the leaf axils.
    3. Plants conspicuously whitish; leaves erect. 17. *P. beringiensis*
    3. Plants green, reddish or black; leaves erect or spreading.
      4. Gemmae translucent orange-red; leaf primordia the same color as the body. 13. *P. pseudo-barbula*
      4. Gemmae opaque, reddish to orange or green, sometimes black; primordia green or pale.
        5. Gemmae cylindrical to oblong, reddish when moist; leaf primordia green and conspicuous, scattered on the body and at the apex. 18. *P. drummondii*
        5. Gemmae elliptic to ovoid, orange when moist (often black when dried); primordia pale, stiffly triangular, mostly restricted to the apex. 19. *P. filum*
  2. Gemmae arising in clusters.
    6. Gemmae spheric to short-oblong, hardly longer than wide.
      7. Primordia of gemmae triangular-laminate, forming a dome over the apex. 22. *P. bulbifera*
      7. Primordia of some or all gemmae peglike (just 1–2 cells broad at the base), erect or ± incurved over the apex.
        8. Gemmae yellow or brown, isodiametric or nearly so. 26. *P. camptotrachela*
        8. Gemmae orange or red, a little longer than wide.
          9. Plants glossy (arctic). 23. *P. andrewsii*
          9. Plants dull (tropical). 12. *P. richardsii*
    6. Gemmae oblong, obconic or ± elongate and vermicular.
      10. Gemmae small (about 110 μm) and orange-red, with the primordia peglike and incurved. go to 8
      10. Gemmae larger, oblong, obconic or linear-vermicular.
        11. Plants glossy.

12. Leaf primordia laminate, at least 3–4 cells broad at the base.
13. Gemmae oblong or obconic. 20. *P. andalusica*
13. Gemmae linear-cylindrical. 21. *P. tundrae*
12. Leaf primordia peglike, 1–2 cells broad at the base (gemmae linear-vermicular). 24. *P. proligera*
11. Plants dull.
14. Gemmae linear-vermicular with one primordium, less commonly oblong with 2–4 primordia (tropical and subtropical). 11. *P. papillosa*
14. Gemmae oblong or obconic to linear-obconic.
15. Stems mostly simple; gemmae linear, obconic or oblong, green, yellow, hyaline or orange (temperate and subarctic North America). 25. *P. annotina*
15. Stems often forking, gemmae broadly oblong or ovoid, reddish-orange (Mexico). 13. *P. pseudo-barbula*
1. Plants without axillary gemmae.
16. Rhizoidal tubers obviously present.
17. Plants shiny yellow-green; cells laxly and broadly rhomboidal; tubers red (Mexico). 36. *P. integra*
17. Plants dull or somewhat glossy green; cells linear rhomboidal, tubers yellow, orange or orange-brown (temperate North America). 28. *P. lescuriana*
16. Tubers lacking.
18. Leaf margins strongly recurved.
19. Stems red, leaves longly lanceolate; cells linear-hexagonal, thin-walled. 10. *P. crudoides*
19. Stems green, leaves lanceolate; cells rhomboidal, rather thick-walled, sometimes porose. 15. *P. cardotii*
18. Leaf margins plane (except the perichaetial bracts).
20. Cells broad, 13 μm or more wide.
21. Plants dull whitish, in calcareous seepy or wet areas. 29. *P. wahlenbergii*
21. Plants yellow-green, reddish or blackish, at least below, in calcareous or acidic, usually wet sites.
22. Plants often robust, to 1 cm or more high, often blackish below and pale green just near the tips. 9. *P. obtusifolia*
22. Plants slender, 3–8 mm high, yellowish or reddish.
23. Plants slender, yellowish, somewhat glossy. 30. *P. melanodon*
23. Plants tiny, populations rarely consisting of more than a few stems, reddish. 31. *P. atropurpurea*
20. Cells narrow, 6–10(–12) μm wide.
24. Cells conspicuously thick-walled.
25. Plants dioicous; leaves nearly entire. 1. *P. sphagnicola*
25. Plants paroicous; leaves ± serrate near the apex. 2. *P. nutans* or 3. *P. elongata*
24. Cells with thin to firm walls.
26. Plants whitish, with the leaves often erect and seriate.
27. Plants slender, to 1 cm high. 32. *P. brevinervis*
27. Plants medium size to robust.
28. Leaves erect and often seriate, lanceolate. 6a. *P. bolanderi* var. *seriata*
28. Leaves ± spreading, not seriate, broadly lanceolate to elliptic. 4. *P. cruda*
26. Plants shiny or dull green, the leaves sometimes erect but not whitish.
29. Plants paroicous.
30. Plants dull or slightly glossy, pale green, 1.5–3.5 cm high (Mexico, Central America). 5. *P. oerstediana*
30. Plants, very glossy, green or pale green, 0.5–2.0 mm high.
31. Leaves long-laneolate, erect, coarsely serrate near the apex. 7. *P. longicollis*
31. Leaves broadly lanceolate, spreading to erect-spreading, serrate or serrulate near the apex. 4. *P. cruda*
29. Plants dioicous.
32. Leaves widespreading, narrowly lanceolate; perigonial bracts very long-acuminate, to 6 mm long. 35. *P. longibracteata*
32. Leaves erect to ± spreading, lanceolate or broadly lanceolate; perigonial bracts shorter, to 3–4 mm.
33. Plants robust; leaves broadly acute to rounded, long-decurrent, those low on the stem often pink. 14. *P.ludwigii*

33. Plants slender to medium size; leaves acute, shortly or not at all decurrent, lower leaves green (all leaves ± reddish in *P. columbica*).
   34. Plants high in the mountains or in the north.
      35. Stems red.
         36. Plants slender with erect-appressed leaves. 33. *P. vexans*
         36. Plants medium size with erect-spreading, soft-appearing leaves. 16. *P. erecta*
      35. Stems green, orange or brown.
         37. Plants of South and Central America. 8. *P. polycarpa*
         37. Plants of the western United States and Canada. 6. *P. bolanderi*
   34. Plants at or near sea level.
      38. Plants very glossy light green. 27. *P. pacifica*
      38. Plants dull or slightly glossy, green or reddish.
         39. Plants dull or slightly glossy, green; perigonial bracts erect or erect-spreading. 28. *P. lescuriana*
         39. Plant dull reddish; perigonial bracts wide-spreading. 34. *P. columbica*

KEY TO PLANTS BEARING SPOROPHYTES

1. Exothecial cells plainly bulging.
   2. Gemmae red or orange, shortly oblong to isodiametric; leaf primordia incurved. 12. *P. richardsii*
   2. Gemmae green, yellow, pink or hyaline, linear-vermicular or less commonly oblong; primordia erect, rarely poorly developed and incurved. 11. *P. papillosa*
1. Exothecial cells not bulging.
   3. Annulus absent; exothecial cells little or no longer than wide.
      4. Cells laxly and broadly rhomboidal, 12 μm or more wide.
         5. Plants tiny (2–6 mm), often reddish; stomates superficial or somewhat immersed; cells of perichaetial bracts narrow (6–10 μm). 30. *P. atropurpurea*
         5. Plants small to robust (5–35 mm), yellowish or whitish-green; most stomates deeply immersed; cells or perichaetial leaves broad, 12–20 μm broad.
            6. Plants pale, whitish-green, 1–5 cm high. 28. *P. wahlenbergii*
            6. Plants yellowish glossy-green, 0.5–1.0 cm high. 29. *P. melanodon*
      4. Cells linear-hexagonal, 6–10 μm wide.
         7. Plants robust; leaves wide-spreading; perigonial bracts long-acuminate, to 6 mm long. 34. *P. longibracteata*
         7. Plants slender; leaves erect to erect-spreading; perigonial bracts shorter, to 3–4 mm long.
            8. Stomates superficial or slightly sunken.
               9. Stems elongate, to 1 cm or more high; leaves erect, whitish; cells of all leaves linear, 6–9 μm wide. 31. *P. brevinervis*
               9. Stems short, 2–6 mm; leaves few, ± spreading (except perichaetial bracts); cells of leaves on sterile plants or lower stem leaves broadly hexagonal, 10–11 μm or more wide. 30. *P. atropurpurea*
            8. Stomates ± deeply immersed.
               10. Stems red, leaves small and erect, glossy green. 32. *P. vexans*
               10. Stems green to orange; leaves larger, spreading, dull, often reddish. 33. *P. columbica*
   3. Annulus present; exothecial cells elongate-rectangular.
      11. Capsule erect; basal membrane low; segments narrow or rudimentary, not keeled.
         12. Endostome segments long, ± perforate; leaf margins recurved; cells rhombic, thick-walled. 15. *P. cardotii*
         12. Endostome segments variously reduced to absent; leaf margins plane; cells linear-rhomboidal; thin-walled. 16. *P. erecta*
      11. Capsule variously inclined; basal membrane low to high; segments broad and keeled or reduced.
         13. Exothecial cells long-rectangular, 60–90 μm long, with straight or slightly sinuose walls.
            14. Endostome segments narrowly or not at all split along the keel; cilia rudimentary or absent, rarely long.

15. Exostome teeth yellowish-white, coarsely papillose from apex to base. 10. *P. crudoides*
15. Exostome teeth brown to yellow-brown or hyaline, more coarsely papillose in the upper ½–⅔ than below.
    16. Some or all plants with more than one seta per inflorescence. 8. *P. polycarpa*
    16. Plants with one seta per inflorescence.
        17. Plants with gemmae; exostome teeth ± blunt, papillose in the upper half, nearly smooth below. 13. *P. pseudo-barbula*
        17. Plants without gemmae; exostome teeth acute or acuminate, coarsely papillose in the upper ⅓, gradually less papillose below.
            18. Plants dull; leaf cells thick-walled.
                19. Capsule 4–7 mm long; basal membrane ⅓–½ the exostome length; segments keeled. 3. *P. elongata*
                19. Capsule 2–4 mm long; basal membrane to ⅓ the exostome length; segments scarcely keeled, often irregular. 3a. *P. elongata* var. *greenii*
            18. Plants ± glossy; cells thin-walled.
                20. Plants dioicous; leaves serrulate to serrate at the apex. 6. *P. bolanderi*
                20. Plants paroicous; leaves coarsely serrate at the apex.
                    21. Plants very glossy (Canada and the U.S.). 7. *P. longicollis*
                    21. Plants slightly glossy, pale green (Mexico and Central America). 5. *P. oerstediana*

14. Endostome segments broadly split along the keel; cilia long.
    22. Plants dioicous.
        23. Plants growing with *Sphagnum*; leaves not decurrent; cells with thickened walls. 1. *P. sphagnicola*
        23. Plants on alpine or subalpine soil; leaves longly decurrent; cells with thin to firm walls. 14. *P. ludwigii*
    22. Plants paroicous.
        24. Basal membrane low; segments narrow, scarcely keeled (though broadly perforate); cells lax and thin-walled, 12–20 μm wide. 9. *P. obtusifolia*
        24. Basal membrane ½ the exostome length; segments broad and keeled; cells linear, 6–10 μm wide.
            25. Leaves dull; cells with thickened walls. 2. *P. nutans*
            25. Leaves slightly to strongly glossy; cells with thin walls.
                26. Leaves broady lanceolate to elliptical, serrulate to serrate at the apex. 4. *P. cruda*
                26. Leaves long-lanceolate, coarsely serrate at the apex. 5. *P. oerstediana*

13. Exothecial cells short rectangular, 25–60 μm long; with strongly sinuose walls.
    27. Plants with axillary gemmae. Species 18–26
    27. Plants without axillary gemmae (rhizoidal tubers sometimes present)
        28. Plants robust; leaves longly decurrent; costa of perichaetial bracts much broadened at the base. 14. *P. ludwigii*
        28. Plants slender; leaves little or not at all decurrent; costa of perichaetial bracts not much broadened at the base.
            29. Plants very glossy; leaves coarsely serrate at the apex; cells 110–180 μm long. 27. *P. pacifica*
            29. Plants not or slightly glossy; leaves serrulate to serrate at the apex; cells 65–120 μm long. 28. *P. lescuriana*

1. **Pohlia sphagnicola** (B. & S.) Lindb. & Arn., K. Svensk. Vet. Ak. Handl. 23: 53. 1890.

Bryum sphagnicola B. & S. *in* B. S. G., Bryol Eur. 4: 158. 1846. (Lectotype: BM–Schimp.).

Webera sphagnicola (B. & S.) Schimp., Coroll. 6. 1856.

Slender, dull-green plants generally scattered among *Sphagnum*. Stems 10–30 mm, simple or forking when sterile, simple or rarely innovating below the inflorescence when fertile; leaves erect-spreading, distant, lanceolate, 1.0–1.6 mm long, entire to serrulae at the apices; upper cells hexagonal to rhomboidal, 25–60 μm long, 6–9 μm wide, thick-walled. Dioicous; perichaetial bracts to 3.5 mm long; perigonial bracts ± long-acuminate, erect to erect-spreading. Capsules inclined 90–145° from vertical, cylindric-pyriform, 3–5 mm long; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute to apiculate; exostome teeth orange-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 10–15 μm, almost smooth. Fig. 1.

Restricted to *Sphagnum* hummocks in bogs and fens; near sea level or montane. Northern Asia, Europe and North America; Oregon, Washington, Alberta, Manitoba, Quebec, Nova Scotia, Prince Edward Island, Newfoundland; Greenland. Map. 1.

Pohlia sphagnicola is circumboreal, but apparently rare throughout its range. It is restricted to *Sphagnum* hummocks but even there it is far less common than *P. nutans.* Habitat alone is not diagnostic for *P. sphagnicola*; in fact, Hedwig's type of *P. nutans* is mixed with a bit of *Sphagnum.* Bruch, Schimper and Gümbel described a variety *sphagnetorum* for *P. nutans* to cover forms growing with *Sphagnum* since they often have long stems and distant leaves.

Pohlia sphagnicola differs from *P. nutans* in having entire or weakly serrulate leaves, shorter cells, and smaller, more nearly smooth spores, in addition to dioicous inflorescences. The two are no doubt closely related, but the differences are, for the most part, consistent (Fig. 2). In an unpublished study at the University of Alberta, R. Belland made the same conclusions using different quantitative methods.

2. **Pohlia nutans** (Hedw.) Lindb., Musci Scand. 18. 1879.

Webera nutans Hedw., Spec. Musc. 168. 1801. (Lectotype: G: Hedw.–Schwaegr.).

Bryum trichodes Hedw., Spec. Mus. 168. 1801 (*nom. nud. in synon.—W. nutans* Hedw.).

B. interruptum Dicks., Pl. Crypt. Brit. fasc. 4. 13. 11f. 6. 1801. (Lectotype: BM–Dicks.).

B. nigricans Dicks., Pl. Crypt. Brit. fasc. 4. 15. 11f. 10. 1801. (Lectotype: BM–Dicks.).

B. sericeum Huds. *ex* With., Syst. Arr. Brit. Pl. ed. 4, 3: 822. 1801 (*nom. illeg. incl. spec. prior—W. nutans*).

Hypnum nutans (Hedw.) Web. & Mohr, Ind. Mus. Pl. Crypt. 3. 1803.

Bryum nutans (Hedw.) Turn., Musc. Hib. 117. 1804.

Webera bicolor Hoppe & Hornsch. *ex* Hornsch. 2: 102. 1819. (?Isotype: G: Hedw.–Schwaegr.).

Bryum insulare Houtt. *ex* Steud.,[1] Nomencl. Bot. 2: 88. 1924 (*nom. nud. in synon.—W. nutans* Hedw.).

Bryum subdenticulatum Brid., Bryol. Univ. 1: 634. 1826. (Lectotype: B–Brid.; Isotype: G: Hedw.–Schwaegr.).

Webera strangulata Nees *ex* Hueb., Musc. Germ. 428. 1833. (?Isotype: BM–Hampe).

Lamprophyllum nutans (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 25. 1871.

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[1] Article 46c of the international code of botanical nomenclature states that *ex* is appropriate in author citations only where the name was validly published. However, *ex* is used in this and similar citations for bibliographic completeness.

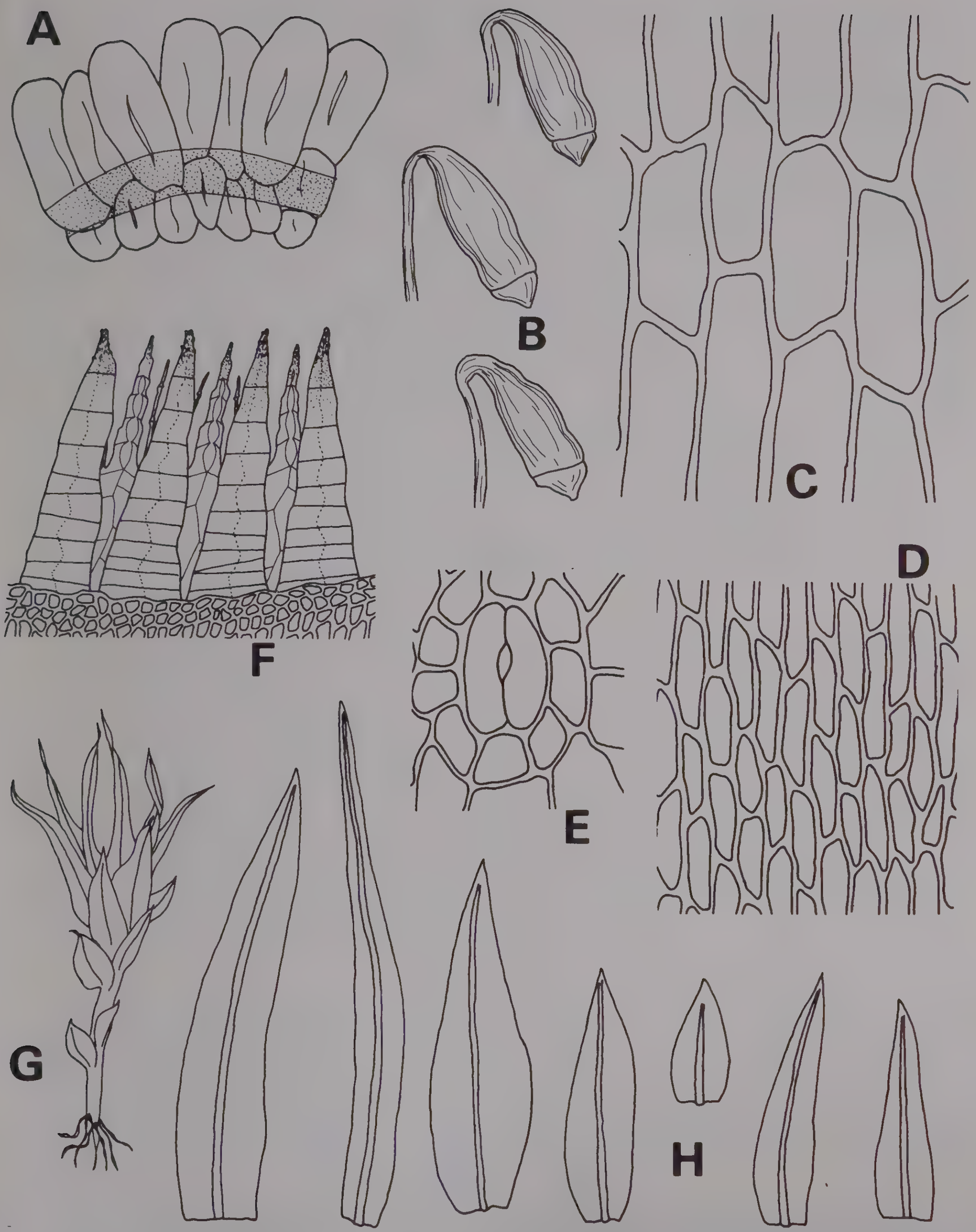


FIG. 1. *Pohlia sphagnicola.* A. Annulus, ×290. B. Capsules, ×15. C. Exothecial cells, ×290. D. Upper leaf cells, ×290. E. Stomate, ×290. F. Peristome, ×80. G. Male plant, ×16. H. Leaves. ×22.

Webera canaliculata C. Müll. & Kindb. *in* Macoun, Cat. Canad. Pl. 6: 113. 1892. (Lectotype: S–Kindb.; Isotype: BH).

Bryum cucullatiforme Kindb., Eur. N. Am. Bryin. 2: 387. 1897. (Lectotype: S–Kindb.: Isotype: BH).

Bryum nutans ssp. *macounii* Kindb., Eur. N. Am. Bryin. 2: 385. 1897. (Lectotype: S–Kindb.; Isotype: BH).

B. nutans ssp. *canaliculatum* (C. Müll. & Kindb. *in* Macoun) Kindb., Eur. N. Am. Bryin 2: 385. 1897.

Bryum canaliculatum (C. Müll. & Kindb. *in* Macoun) C. Müll., Gen. Musc. Fr. 221. 1901.

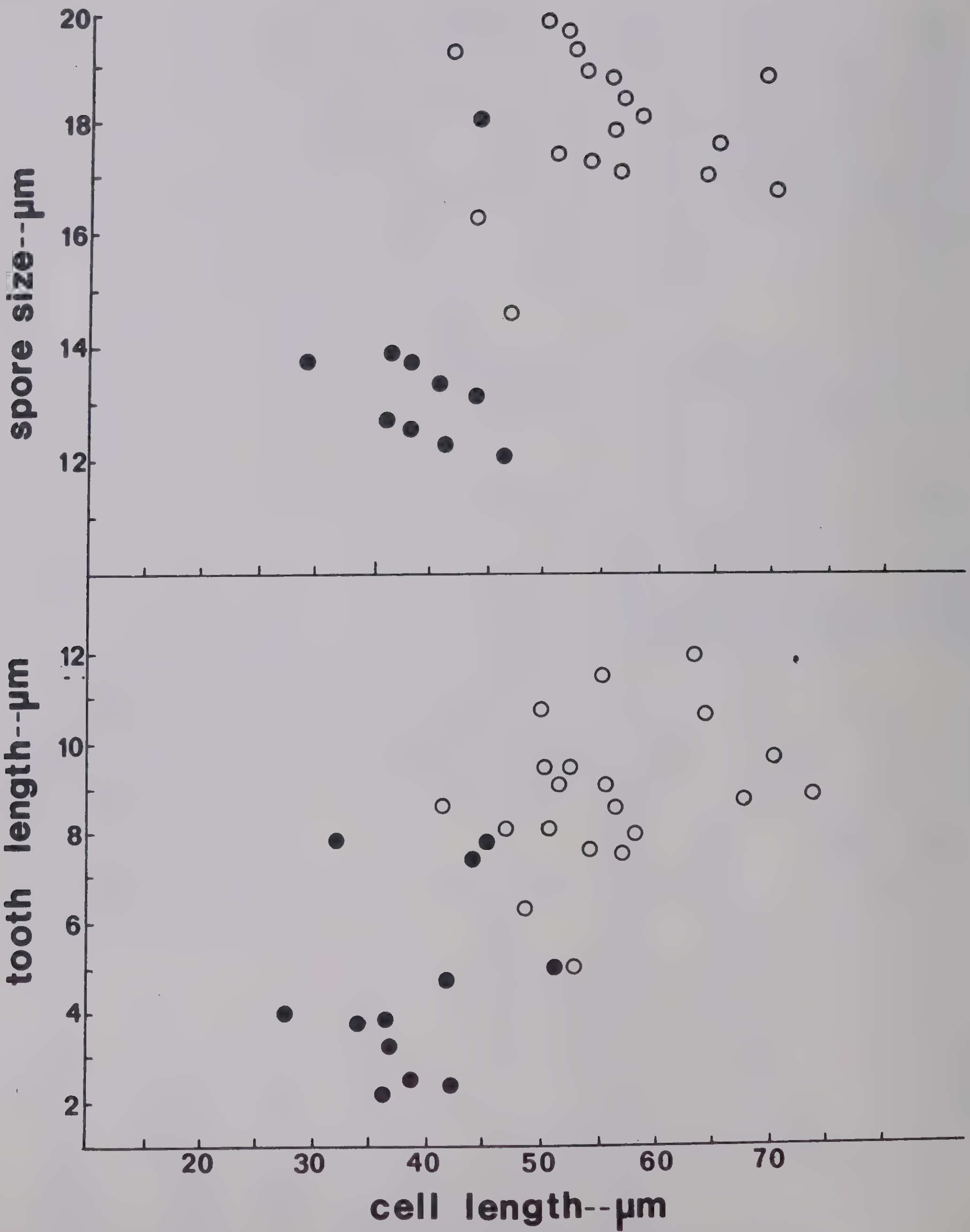


FIG. 2. Scatter diagrams comparing *Pohlia nutans* and *P. sphagnicola* with respect to leaf cell length, length of teeth on leaf margins, and spore diameter.

Bryum pertenellum Bryhn. & Ryan *in* Bryhn, Rep. Sec. Norw. Arctic Exp. Fram no. 11. 1906. (Lectotype: O).

Pohlia polygama Kindb., Rev. Bryol. 34: 92. 1907. (Lectotype: S–Kindb.).

Bryum graniticum Warnst. & Geh. *ex* Podp., Mag. Bot. Lapok. 18: 21. 1919. (*nom. inval. in synon.*—*P. nutans*).

Pohlia subdenticulata (Brid.) Podp. *in* Gyoerffy, Mag. Bot. Lapok. 18: 21. 1919.

Webera polygama (Kindb.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 360. 1924.

Bryum implexum Sw. *ex* Podp., Act. Ac. Sc. Nat. Morav. 17: 91. 1945 (*nom. nud. in synon.*—*P. nutans*).

Bryum compactum Aust., Bot. Gaz. 2: 111. 1877. (Lectotype: NY).

Slender to medium-size, dull-green plants scattered singly or forming extensive turfs. Stems 4–30 mm, simple or forking when sterile, simple or rarely innovating below the inflorescence when fertile. Leaves erect to spreading, crowded to distant, lanceolate, 0.8–1.6 mm long, serrate to serrulate near the apices; upper cells linear-rhomboidal, 50–90 μm long, thick-walled. Paroicous; perichaetial bracts to 4.0(–5.0) mm long. Capsules inclined 90–145° from vertical, cylindric-pyriform, 3–5 mm long; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute to apiculate; exostome teeth yellow to orange-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline, rarely yellow-brown; basal membrane ½ exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 16–22 μm, distinctly roughened. Fig. 3.

In rock crevices, on mineral soil, rotting logs, tree bases, roadbanks and mixed with *Sphagnum*; sea level to alpine. Across Canada and the northern United States, Europe and Asia; widespread at high latitudes of the Southern Hemisphere; south in North America to Maryland, Virginia, Missouri, Arizona, New Mexico and California (reported from Georgia and Arkansas); known in Mexico from only two localities (Potosí and Nevado de Toluca); apparently absent from the New World tropics. Map 2.

Exsiccati: Austin, Musci Appal. 510 as *B. elongatum* (UBC); Bauer, Musci Eur. Exs. 318–320 as *P. nutans* (ALTA), 909–910 as *P. nutans* (WTU), 911 as *P. nutans* f. *umbrosa* (WTU), 1095, 1096a & b as *P. nutans* v. *caespitosa* (WTU), 1097 as *P. nutans* v. *subglobosa* (WTU); Bauer, Bryoth. Bohem. 234 as *W. nutans* v. *sphagnetorum* (WTU); Boros, Plantae Hungar. Exs. 878 (CAS); Brotherus, Bryoth. Fenn. 335 as *P. nutans* v. *longiseta* (WTU); Drummond, Musci Amer. 262 as *B. nutans* (MICH); Grout, N. Am. Musci Perf. 23 as *P. nutans* (UC, CAS); Holzinger, Musci Acro. Bor.-Am. 143a & b as *W. commutata* (MICH, NY), 166 as *W. nutans* (MICH, UC, WTU), 167 as *W. nutans* v. *subdenticulata*, (MICH, UC, WTU), 524–525 as *W. nutans* (MICH, UC, WTU); Kobsch, Bryoth. Sax. 50 as *P. nutans* (MICH), 421 as *B. nutans* f. *elata* (MICH), 526 as *P. nutans* v. *caespitosa* (MICH); Macoun, Canad. Musci 160 as *W. nutans* (UC); Noguchi, Musci Jap. 840 as *P. nutans* (MICH); Rabenhorst, Bryoth. Eur. 329b as *B. nutans* (UC), 584 as *B. nutans* (UC); Sull. & Lesq., Musci Bor.-Am. (ed. 1) 179 as *B. nutans* (MICH), 178 as *B. nutans* (MICH), ed. 2, 267 as *B. nutans* (UC, MICH), 268 as *B. nutans* (MICH); Warnstorf, Märk. Laubm. 64 as *W. nutans* (CAS), 175 as *W. nutans* v. *sphagnitorum* (CAS).

Pohlia nutans is characterized by its thick-walled cells giving the plants a dull appearance, and paroicous inflorescence. The endostome is well-developed with keeled, broadly perforate segments and nodulose cilia. When sterile, plants are difficult to distinguish from *P. elongata,* except by habitat and range. Even some fruiting specimens approach *P. elongata* in having more narrowly perforate endostome segments, and (or) short cilia, making a definite determination impossible.

One poorly developed specimen from central Mexico (Nevado de Toluca, *Rzedowski 21676,* US) is unusual in having a yellow-brown endostome with rather narrowly split segments. The type of *Webera luisieri* Dix. from Madeira also appears to be decrepit *P. nutans* with a yellow endostome. I do not consider such forms worthy of nomenclatural recognition, at least on the basis of the rather poor material available.

Although rare, a few collections otherwise referable to *P. nutans* appear to be dioicous. Crum and Anderson (1981) reported one such New York collection (*Smith & Glider 43837*, as questionable *P. sphagnicola. Pohlia schimperi* (C. Müll.) Andr. is said to differ from *P. nutans* in its lush habit, red color, and dioicous inflorescence. North American specimens determined by Andrews as *P. schimperi* are all rather unexceptional *P. nutans,* and I have seen only one Alaskan collection (Peters Lake, *Steere 650725–21*) that agrees with the type of *P. schimperi.* The differences between the two species are not convincing. I have excluded *P. schimperi* from the North American flora, but have not placed it in the synonymy of *P. nutans* pending study of more collections. The many infra-

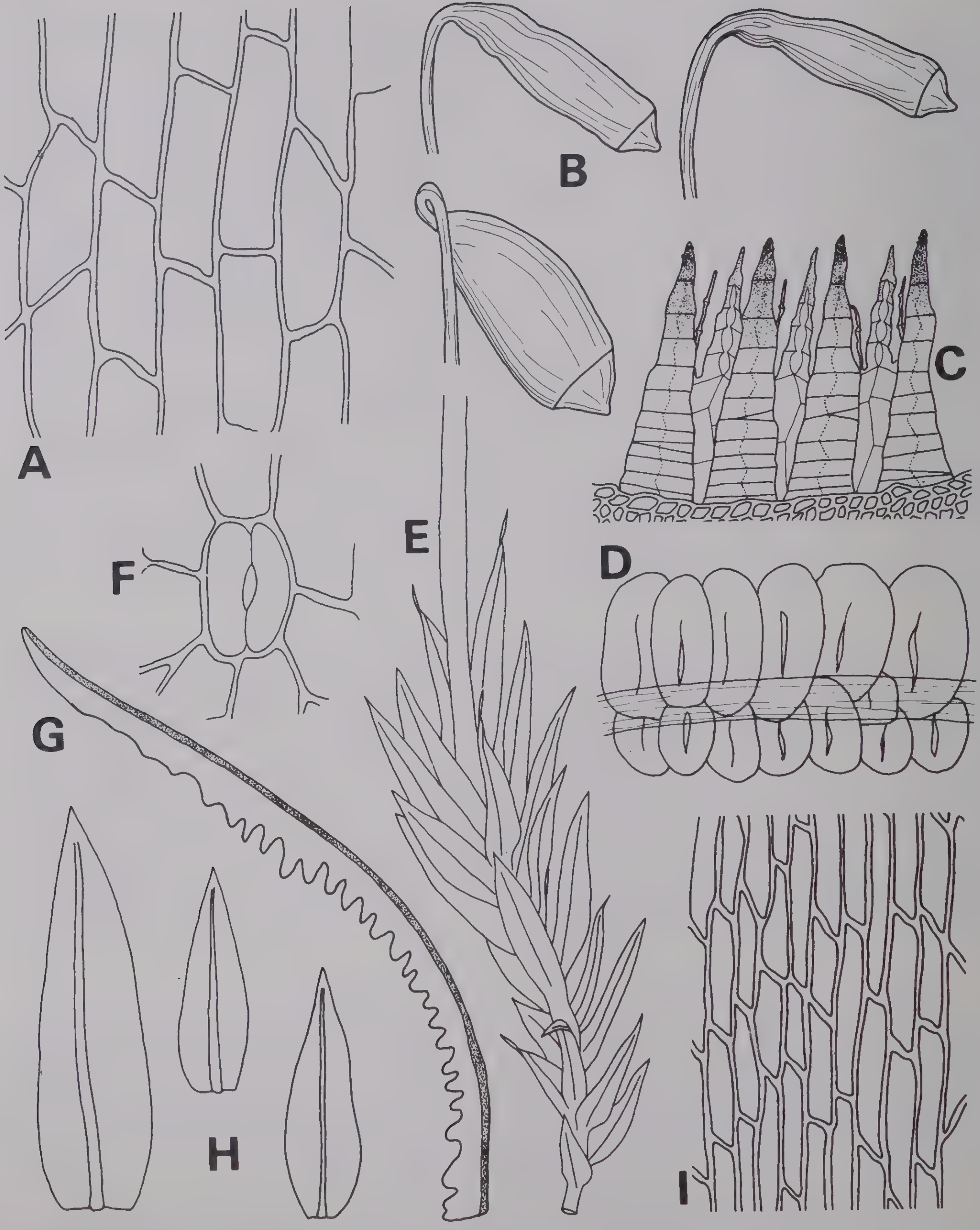


FIG. 3. *Pohlia nutans*. A. Exothecial cells, ×290. B. Capsules, ×15. C. Peristome, ×80. D. Annulus, ×290. E. Female plant, ×5. F. Stomate, ×290. G. Exostome tooth, lateral view showing relative thickness of dorsal and ventral plates and trabecula, ×250. H. Leaves, ×22. I. Upper leaf cells, ×290.

specific taxa proposed under *P. nutans* should be evaluated in the light of a world-wide study.

3. **Pohlia elongata** Hedw., Spec. Musc. 171. 1801.

Bryum cylindricum Dicks., Pl. Crypt. Brit. Fasc. 4, 12. 11f. 4. 1801. (Lectotype: BM–Dicks.).

Bryum elongatum (Hedw.) With., Syst. Arr. Brit. Pl. ed. 4, 3: 815. 1801.

Leskea elongata (Hedw.) Web. & Mohr, Ind. Musc. Pl. Crypt. 3. 1803.

Mnium elongatum (Hedw.) P. Beauv., Prodr. 75. 1805.

M. pohlia Hoff. *ex* P. Beauv., Prodr. 75. 1805. (*nom. nud. in synon.—M. elongatum*).

Pohlia arcuata Hoppe & Hornsch. *ex* Hornsch., Flora 2: 98. 1819. (Lectotype: GZU-Hoppe).

P. brachycarpa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 96. 1819. (Lectotype: GZU-Hoppe).

P. tenella Hoppe & Hornsch. *ex* Hornsch., Flora 2: 95. 1819. (Lectotype: GZU-Hoppe).

Webera caespitosa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 102. 1819. (Lectotype: GZU-Hoppe).

Pohlia acuminata Hoppe & Hornsch. *ex* Hornsch., Flora 2: 94. 1819. (Lectotype: GZU: Hoppe; Isotype: G: Hedw.–Schwaegr.).

P. polymorpha Hoppe & Hornsch. *ex* Hornsch., Flora 1: 100. 1819. (Lectotype: GZU: Hoppe).

P. affinis Hoppe & Hornsch. *ex* Hornsch., Flora 2: 97. 1819. (Lectotype: GZU: Hoppe).

P. pulchella Hoppe & Hornsch. *ex* Hornsch., Flora 2: 95. 1819. (Lectotype: GZU: Hoppe; Isotype: G: Hedw.–Schwaegr.).

P. xanthocarpa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 97. 1819. (Lectotype: GZU: Hoppe).

Webera macrocarpa Hoppe & Hornsch. *ex* Hornsch., Flora 2: 104. 1819. (Isotype: G: Hedw.–Schwaegr.).

Pohlia cylindrica (Dicks.) Hornsch., Flora 2: 93. 1819.

P. recognita Reichenb., Flora 5: 540. 1822 (*nom. nud. in synon.—P. elongata*).

P. minor var. *affinis* (Hoppe & Hornsch. *ex* Hornsch.) Brid., Bryol. Univ. 7: 612. 1826.

P. elongata var. *cylindrica* (Dicks.) Brid., Bryol. Univ. 7: 610. 1826.

Webera alpina var. *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Brid., Bryol. Univ. 7: 627. 1826.

Webera elongata var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Schwaegr., Suppl. Spec. Pl. ed. 4, 5: 49. 1830.

P. elongata var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 473. 1833.

P. polymorpha var. *affinis* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 470. 1833.

P. polymorpha var *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 470. 1833.

P. brachycarpa var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Schwaegr. *ex* Hueb., Musc. Germ. 717. 1833.

Bryum boissieri D. Not., Syll. 134. 1838. (Lectotype: R: De Not.).

B. polymorphum (Hoppe & Hornsch. *ex* Hornsch.) Hartm., Handb. Skand. Fl. ed. 3: 296. 1838.

B. elongatum var. *macrocarpum* (Hoppe & Hornsch. *ex* Hornsch.) B. & S. *in* B. S. G., Bryol. Eur. 4: 102. 1839.

B. acuminatum (Hoppe & Hornsch. *ex* Hornsch.) B. & S., Bryol. Eur. 4: 91. 1839.

Bryum alpinum var. *macrocarpum* (Hoppe & Hornsch. *ex* Hornsch.) Lesq., Mem. Soc. Sc. Neuchâtel. 3: 37. 1845.

?*B. integridens* C. Müll., Syn. 1: 338. 1848 (type not seen).

B. spectabile C. Müll., Syn. 2: 583. 1851. (Lectotype: H–Br.).

Webera acuminata (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

W. acuminata var *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

W. acuminata var. *tenella* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

W. elongata var. *macrocarpa* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

Webera polymorpha (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

W. polymorpha var. *affinis* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

W. polymorpha var. *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

Lamprophyllum elongatum (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 27. 1871.

W. spectabilis (C. Müll.) Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872.

?*W. integridens* (C. Müll.) Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872.

W. cylindrica Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872. (Isotype: NY; ?Isotype: BM).

Bryum cylindricum Mont. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872 (*nom. inval. in synon.–W. cylindrica*).

Webera muelleriana Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 196. 1872. (?Isotype: BM: Schimp.).

W. gracilicarpa Hampe, Vid. Medd. Naturh. For. Kjoebenh. ser. 3, 6: 149. 1875.

W. ambigua Limpr., Laubm. Deutschl. 2: 237. 1891. (Lectotype: BP–Limpr.).

B. elongatum ssp. *ambiguum* (Limpr.) Kindb., Eur. N. Am. Bryin. 2: 390. 1890.

B. elongatum ssp. *acuminatum* (Hoppe & Hornsch. *ex* Hornsch.) Kindb., Eur. N. Am. Bryin. 2: 390. 1890.

Bryum muellerianum (Schimp. *ex* Besch.) C. Müll., Gen. Musc. Fr. 220. 1901.

Bryum ambiguum (Limpr.) Kindb. *ex* Par., Ind. Bryol. Suppl. 56. 1900 (*nom. inval. in synon.–B. elongatum* spp. *ambiguum*).

Pohlia ambigua (Limpr.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

P. muelleriana (Schimp. *ex* Besch.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

P. spectabilis (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

?*P. integridens* (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

P. elongata var. *macrocarpa* (Hoppe & Hornsch. *ex* Hornsch.) Herz., Bot. Jahrb. 47: 482. 1912.

P. acuminata var. *tenella* (Hoppe & Hornsch. *ex* Hornsch.) Amann, Fl. Mouss. Suisse 2: 178. 1919.

P. acuminata var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Amann, Fl. Mouss. Suisse 2: 178. 1919.

P. polymorpha var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) C. Jens., Danm. Moss. 2: 392. 1923.

Pohlia zacatecana Williams, Bryol. 26: 33. 4. 1923. (Isotype: US).

Webera zacatecana (Williams) Thér., Smiths. Misc. Coll. 81: 7. 1928.

Webera polymorpha var. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) C. Jens., Skand. Bladmfl. 166. 1939.

Pohlia polymorpha ssp. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Podp., Consp. 331. 1954.

P. polymorpha var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Podp., Consp. 331. 1954.

P. minor var. *tenella* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor var. *arcuata* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor var. *brachycarpa* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor ssp. *acuminata* (Hoppe & Hornsch. *ex* Hornsch.) Wijk & Marg., Taxon 8: 74. 1959.

P. minor var. *pulchella* (Hoppe & Hornsch. *ex* Hornsch.) Dem. & Wilz., Bull. Jard. Bot. Nat. Belg. 48: 449. 1978.

Slender to medium size, dull-green plants forming small populations, often in rock crevices. Stems 5–25 mm, simple or forking when sterile, frequently innovating below the inflorescence when fertile. Leaves erect to erect-spreading, crowded to distant, lanceolate, 0.9–1.7 mm long, serrulate to serrate near the apices; upper cells rhomboidal to linear-hexagonal, 45–85 μm long, thick-walled. Paroicous or rarely autoicous; perichaetial bracts little to strongly differentiated, to 3.5 mm; perigonia in autoicous plants terminal on short to elongate side branches, the perigonial bracts shortly acute. Capsules inclined 10°–90° from vertical, shortly to longly cylindric-pyriform, 3.5–7.0 mm long; exothecial cells elongate-rectangular, 50–110 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute; exostome teeth yellow to brown, acute-triangular, most coarsely papillose near the apex, bordered, trabeculate; endostome hyaline; basal membrane ⅓–½ the exostome length; segments keeled but narrowly perforate; cilia short, absent, rarely long and ± nodulose. Spores 16–23 μm; distinctly roughened. Fig. 4, 5.

Roadbanks and streambanks; frequent in rock crevices in arctic or alpine regions; reportedly epiphytic in New Guinea. Widespread at high latitudes across the three northern continents. In North America, apparently absent from the Cascade-Sierra Nevada system of the western United States, but extending southward in the Appalachians to Tennessee and North Carolina. Ranging in the Rockies from Alaska to Arizona, and extending in the mountains through Mexico, Central America and, through scattered records, to southern South America; Africa, China, Nepal, S. E. Asia, Phillipines, Japan, and New Guinea. Map 3.

Exsiccati: Austin, Musci Appal. (Suppl. 1) 510 as *B. elongatum* (CANM, NY); Bauer, Musci Eur. Exs. 903 as *P. acuminata* (WTU); Bauer, Bryoth. Bohem. 233 as *W. elongata* v. *oder* f. *pseudolongicolla* (BM); Erbar, Crittogam. Ital. 609 as *W. elongata* (UC, NY); Fleischer, Musci Frond. Arch. Indici 285 as *W. brachydontea* (NY); Grout, N. Am. Musci Perf. 398 as *P. elongata* (CANM, MICH, UC); Hartman, Bryac. Scand. 376 as *W. elongata* (BH); Holzinger, Musci Acro. Bor.–Am. 145 as *W. elongata* (CANM, MICH, NY, UC); Husnot, Musci Gall. 461 as *W. elongata* (BH, BM, NY); Macoun, Canad. Musci 521 as *W. acuminata* (MICH), 806 as *W. acuminata* (CANM); Noguchi & Hattori, Musci Jap. 386 as *P. elongata* (ALTA, BH, MICH, NY); Pringle, Plant. Mex. 10623 & 10648 as *W. cylindrica* (MICH, MO); Rabenhorst, Bryoth. Eur. 275 as *W. elongata* (NY, UC), 360 as *W. elongata* (NY, UC); Schultz, Flora Gall. et Germ. Exs. 1185 as *B. elongatum* (BM); Sull. & Lesq., Musci Bor. Amer. (ed. 1) 177 as *B. elongatum* (BH, MICH, NY), (ed. 3) 266 as *B. elongatum* (BH, MICH, NY, UC), 270 as *B. ludwigii* (BH).

Pohlia elongata is distinguished from related species by its (usually) paroicous inflorescence, longly cylindric capsules (4–7 mm), and especially the narrowly or scarcely perforate endostome segments. Unlike *P. longicollis* and *P. bolanderi*, which have similar peristomes, the leaves are dull with cell walls incrassate. The sexuality of *P. elongata* var. *elongata* is almost uniformly paroicous, although a few specimens, including the type of *Webera ambigua* Limpr., are autoicous.

Capsule size and shape are extremely variable. Mexican and Central American plants generally known as *P. spectabilis* are characterized by exceptionally long, narrow capsules. However, other than in exothecial cell length which is obviously correlated in development with capsule length, such plants can scarcely be distinguished consistently from more typical *P. elongata.* Although a somewhat coherent distribution in Mexico and Central and northern South America suggests at least limited genetic distinctiveness for *P. spectabilis*, frequent intergradation makes recognition of two taxa impractical. A specimen from Virginia

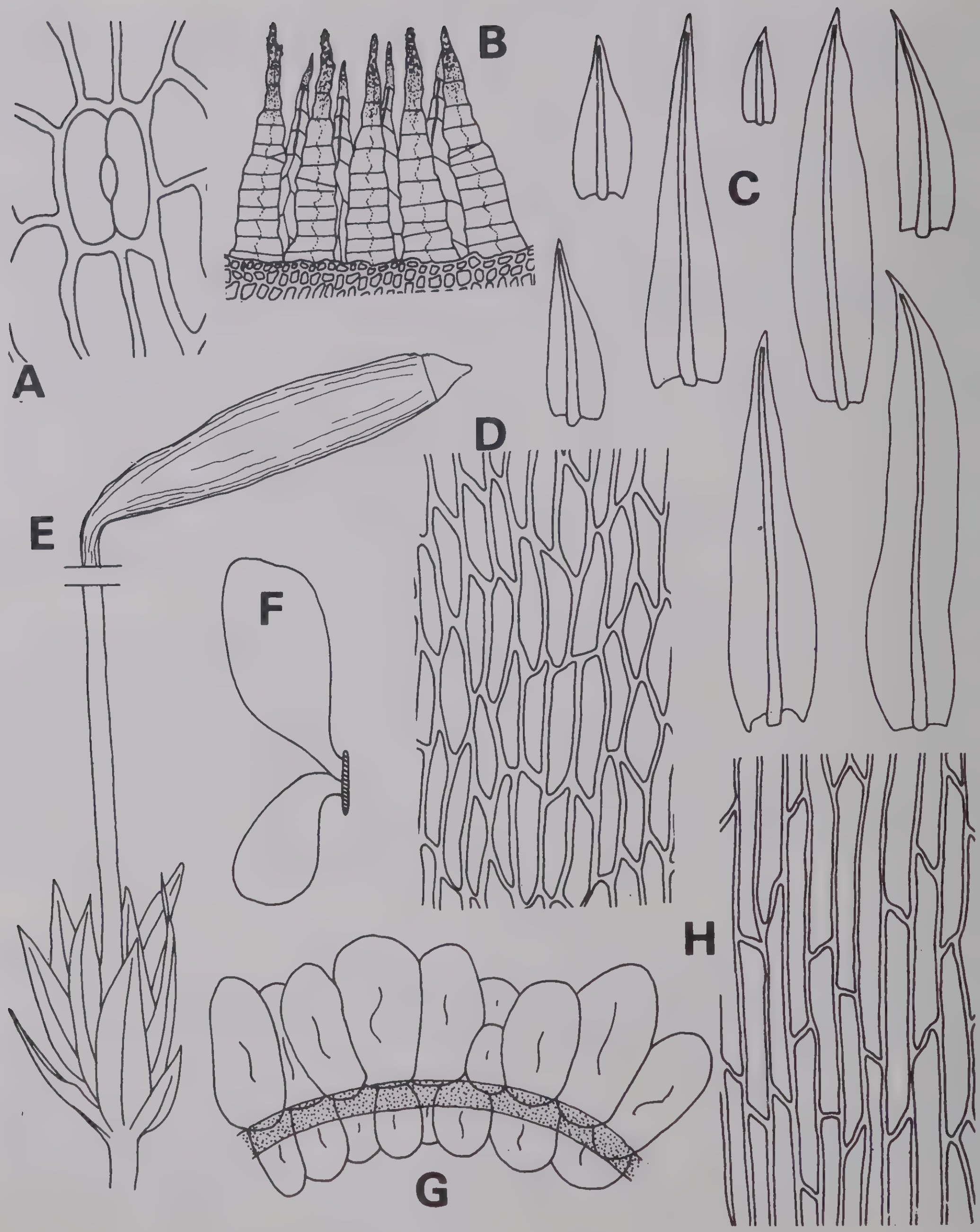


FIG. 4. *Pohlia elongata.* A. Stomate, ×290. B. Peristome, ×80. C. leaves, ×22. D. Upper cells of branch leaf, ×290. E. Habit, ×7. F. Lateral view of annular cells, ×290. G. Annulus, ×290. H. Upper cells of perichaetial bract, ×290.

(*Brown,* 1890, UBC) also approaches *P. spectabilis.* In Mexico, as both the "spectabilis" and typical expressions, *P. elongata* is more common then anywhere else in North America.

At the other extreme, scattered collections of *P. elongata* from arctic, alpine, or other harsh habitats are characterized by a suite of distinctive attributes. These plants can be distinguished as the var. *greenii.*

3b. **Pohlia elongata** var. **greenii** (Brid.) Shaw, comb. nov.

Pohlia minor Schwaegr., Spec. Musc. Suppl. 1: 70. 64. 1816. (Lectotype: G: Hedw.–Schwaegr.; Isotype: B–Brid.).

P. gracilis Hoppe & Hornsch. *ex* Hornsch., Flora 2: 100. 1819. (Lectotype: G: Hedw.–Schwaegr.).

P. polyseta Hoppe & Hornsch. *ex* Hornsch., Flora 2: 99. 1819. (?Isotype: BM).

P. curviseta Hoppe & Hornsch. *ex* Hornsch., Flora 2: 98. 1819. (Lectotype: GZU: Hoppe; ?Isotype: G: Hedw.–Schwaegr.; ?Isotype: NY).

P. greenii Brid., Mant. Musc. 115. 1819. (Lectotype: B: Brid.).

P. minor Schwaegr. var. *greenii* (Brid.) Brid., Bryol. Univ. 1: 612. 1826.

P. elongata var. *minor* (Schwaegr.) Hartm., Handb. Skand. Fl. ed. 2L 336. 1832.

P. polymorpha var. *minor* (Schwaegr.) Hueb., Musc. Germ. 470. 1833.

P. polymorpha var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Hueb., Musc. Germ. 470. 1833.

Bryum elongatum var. *minus* (Schwaegr.) Hartm., Handb. Skand. Fl. ed. 3: 296. 1838.

Webera gracilis (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 65. 1856.

W. acuminata var. *minor* (Schwaegr.) Schimp., Coroll. 64. 1856.

W. acuminata var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Schimp., Coroll. 64. 1856.

Bryum nudicaule Lesq., Mem. Calif. Ac. Sc. 1. 21. 1868.

Webera nudicaulis (Lesq.) Lesq. & James, Man. N. Am. Moss. 220. 1884.

Pohlia polymorpha var. *gracilis* (Hoppe & Hornsch. *ex* Hornsch.) Braithw., Brit. Moss Fl. 2: 145. 1892.

Pohlia nudicaulis (Lesq.) Broth. *ex* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

P. brachycarpa var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Schwaegr. *ex* Par., Ind. Bryol. ed. 2, 5: 105. 1906.

P. acuminata var. *minor* (Schwaegr.) Amann, Fl. Mouss. Suisse 3: 178. 1919.

P. acuminata var. *polyseta* (Hoppe & Hornsch. *ex* Hornsch.) Amann, Fl. Mouss. Suisse 3: 178. 1919.

P. minor var. *gracilis* (Hoppe & Hornsch. *ex* Hornsch.) Wijk et Marg., Taxon 8: 74. 1959.

Tiny, dull-green plants scattered singly or in small populations. Stems very short, with 5–10 leaves. Leaves scarcely 1 mm long, broadly lanceolate; upper cells rhombic, 35–65 μm long, thick-walled. Paroicous, autoicous or rarely dioicous; perichaetial bracts undifferentiated, broadly lanceolate, to 1.5 mm long; perigonia in dioicous plants terminal on short, simple stems, the bracts shortly and broadly acute, erect. Capsules inclined 145°–190° from vertical segments broadly pyriform, 2–3.5 mm long; basal membrane low, up to ⅓ the exostome length, segments often irregular, linear, scarcely keeled, narrowly perforate to entire; cilia absent. Fig. 5.

Rock crevices in tundra areas, less frequently on exposed soil. Alaska, Washington, California, Colorado, Utah, Newfoundland; Greenland. Reported from northern Europe. Map 4.

Although no single character is diagnostic, several morphological attributes distinguish the var. *greenii* from so-called typical expressions: smaller overall size; shorter, broader leaves, more strongly inclined, broader, shorter capsules, low basal membrane, irregular segments, and complete lack of cilia.

Ironically, it is Hoppe and Hornschuch's extensive list of "new species" that provides the most persuasive argument against recognizing the var. *greenii* at the specific level. With over ten taxa, they (Hoppe and Hornschuch *ex* Hornschuch 1819) typified practically every conceivable intermediate between the long and short capsule forms. However, sporophytic and gametophytic differences between the varieties, coupled with geographic differences, warrant separation, at least on the basis of North American plants. Unlike *P. spectabilis,* the var. *greenii*

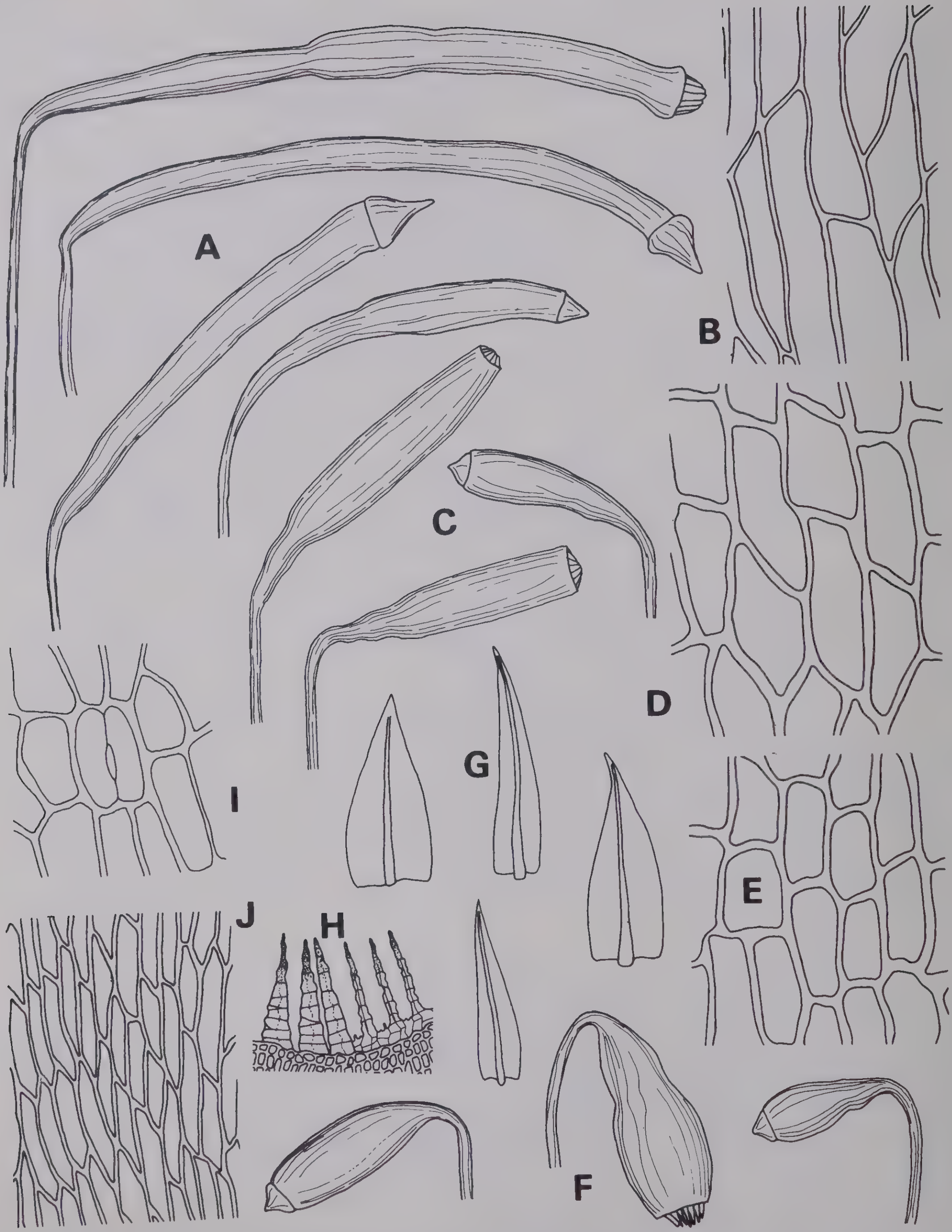


FIG. 5. A–D. *Pohlia elongata* var. *elongata*. A. Capsules, Mexican plants commonly called *P. spectabilis*, ×13. B. Exothecial cells from capsules as in A, ×230. C. Capsules, typical North American plants, ×13. D. Exothecial cells from capsules as in C, ×230. E–J. *Pohlia elongata* var. *greenii*. E. Exothecial cells from capsules as in F, ×230. F. Capsules, ×13. G. Leaves, ×18. H. Peristome, ×58. I. Stomate, ×230. J. Upper leaf cells, ×230.

differs from the var. *elongata* in more than just capsule shape, and notably so in endostome morphology. *Webera carneoides* Dix & Badw. of the Himalayas represents the var. *greenii* at its extreme. The plants are minute, with capsules scarcely longer than wide.

It is difficult to typify the var. *greenii* because so many names are available representing the extensive intergradation that occurs between plants with long and short capsules. Most of the old types are fragmentary and could scarcely endure yet one more peristome dissection. My concept of the var. *greenii* is the short capsule-reduced endostome form at or near its extreme (Fig. 5). Extensive variation in capsule shape is allowed in the var. *elongata.* The names *P. polymorpha* and *P. acuminata* have been used for plants with relatively short capsules. Specimens in Hoppe's herbarium with these names have intermediate to elongate capsules (e.g. Fig. 5c), falling within the range of the var. *elongata.*

4. **Pohlia cruda** (Hedw.) Lindb., Musci Scand. 18. 1879.

Mnium crudum Hedw., Spec. Musc. 189. 1801. (Lectotype: G: Hedw.–Schwaegr.).

Hypnum crudum (Hedw.) Web. & Mohr, Ind. Mus. Pl. Crypt. 3: 1803.

Webera cruda (Hedw.) Fuernr., Flora 12(Ergbl. 2): 35. 1829.

Lamprophyllum crudum (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 87. 1871.

Webera cruda var. *nivalis* Podp. *ex* Herz., Wien. Bot. Zeitschr. 93: 45. 1944. (Lectotype: BRNM).

Robust to slender, shiny, pale whitish-green plants generally forming small populations. Stems 5–20 mm, simple or forking when sterile, usually simple when fertile. Leaves wide-spreading to erect-spreading, distant to crowded, lanceolate to elliptic, sometimes ± asymmetric, 1.0–2.0 mm long, serrate to serrulate at the apices; upper cells linear-rhomboidal, 70–120 μm long, 6–9 μm wide, thin-walled. Paroicous or dioicous; perichaetial bracts variable, lanceolate to linear, to 4.0–5.0 mm long; perigonial bracts longly acuminate, to 5.0 mm long. Capsules inclined 10°–135° from vertical, narrowly or rarely broadly cylindric-pyriform, 4–6 mm long; exothecial cells elongate-rectangular, 40–80 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic; exostome yellow-brown to red-brown; acute-triangular, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 18–26 μm, rather coarsely papillose. Fig. 6.

Soil of roadbanks, streambanks, tundra, often in crevices under rocks or exposed roots; rarely on rotting wood. Circumboreal; across northern North America south to California, Arizona, Tennessee and North Carolina; Mexico (Puebla, Tlaxcala, Mexico); Chile; Antarctica; New Zealand; Auckland Islands; Hawaii; India; Japan; reported from eastern Asia. Map 5.

Exsiccati: Allen, Mosses of the Cascade Mts. 58 as *B. crudum* (MICH); Bauer, Musci Eur. Exs. 311 as *P. cruda* (ALTA); Drummond, Musci Amer. 269 as *B. crudum* (MICH, UC); Grout, N. Am. Musci Perf. 398a as *P. elongata* (MICH), 443a as *P. cruda* (CAS, MICH, UC), 443b as *P. cruda* (MICH); Holmen, Bryoph. Dan. Exs. 155 as *W. cruda* (ALTA, UC); Holzinger, Musci Acro. Bor.–Am. 144 as *W. cruda* v. *minor* (MICH, UC); Kobsch, Bryoth. Sax. 336 as *W. cruda* (MICH); Macoun, Canad. Musci 161 as *W. cruda* (UC), 446 as *W. cruda* (MICH), 637 as *W. micro-apiculata* (MICH); Noguchi, Musci Jap. 1134 as *P. cruda* (MICH); Rabenhorst, Bryoth. Eur. 1024 as *W. cruda* (CAS); Sull. & Lesq., Musci Bor. Am. (ed. 1) 179b as *B. crudum* (MICH); Warnstorf, Märk. Laubm. 270 as *W. cruda* (CAS).

Readily distinguished by its pale, whitish-green color and strong gloss, *P. cruda* is not to be confused with any other *Pohlia.* It is further characterized by the longly cylindric capsules and well-developed endostome with broadly perforate segments and long cilia.

I have seen a few sterile *Pohlia* collections with elongate stems (to 2 cm) and glossy pale-green leaves. These are distinctive, with the leaves lanceolate, erect, and overlapping. One such gathering (N.Y., Westchester Co., *Shaw,* 26 Dec. 1981, MICH) grew on seepy granitic rock in beech-maple forest. The habitat, as well as the aspect of the plants, brought *Mielichhoferia* to mind. In the absence of sporophytes, these are interpreted as *P. cruda,* mostly by default. Ecologically and morphologically this expression is well characterized.

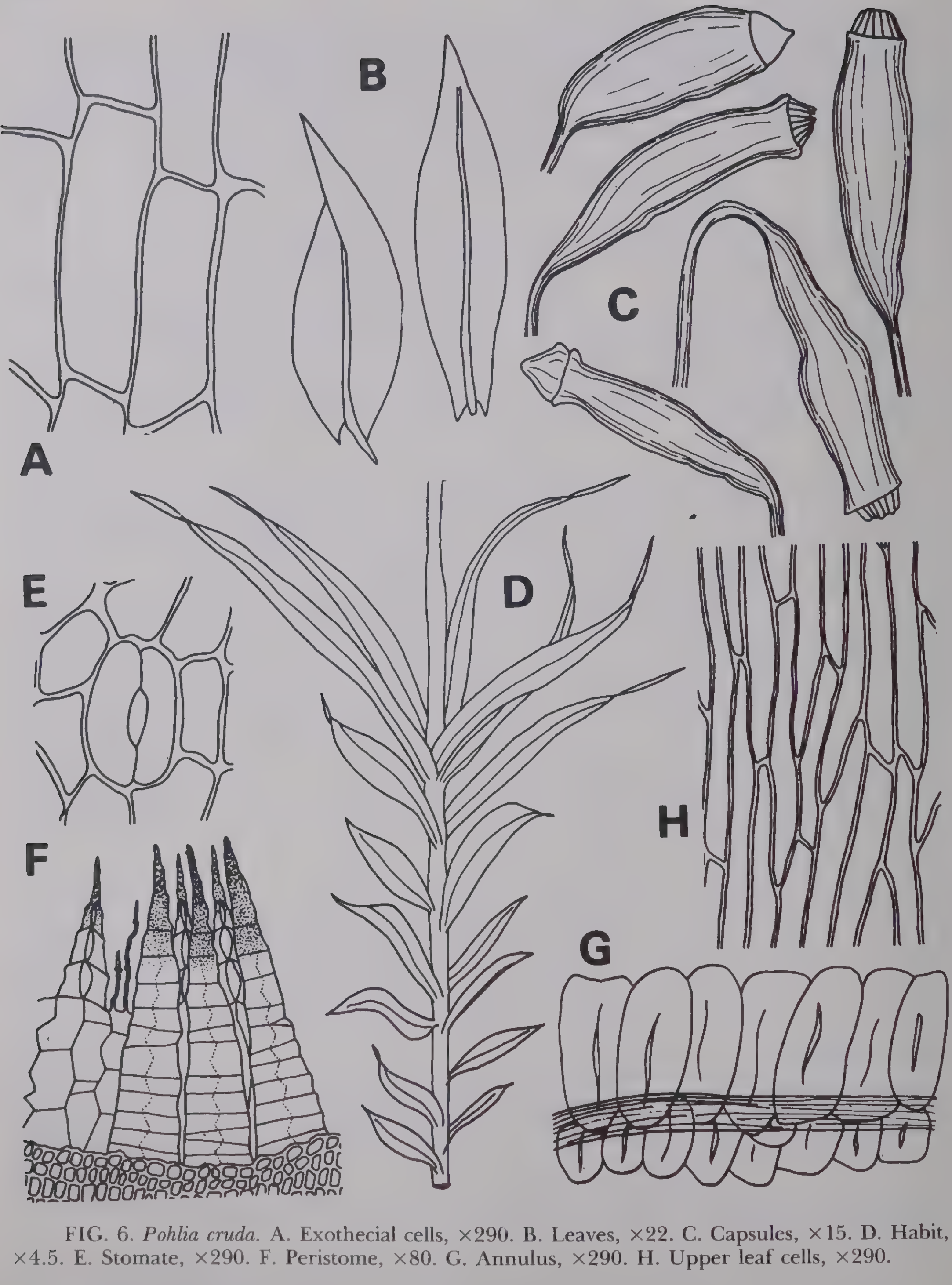


FIG. 6. *Pohlia cruda.* A. Exothecial cells, ×290. B. Leaves, ×22. C. Capsules, ×15. D. Habit, ×4.5. E. Stomate, ×290. F. Peristome, ×80. G. Annulus, ×290. H. Upper leaf cells, ×290.

5. **Pohlia oerstediana** (C. Müll.) Shaw, comb. nov.

Bryum oerstedianum C. Müll., Syn. 2: 583. 1851. (Lectotype: H–Br; Isotype: BM–Hampe).

Webera oerstediana (C. Müll.) Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 128. 1875.

Bryum seleri C. Müll., Bull. Herb. Boiss. 5: 181. 1897. (Lectotype: H–Br).

Pohlia seleri (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

Webera orizabensis Card., Rev. Bryol. 40: 38. 1913. (Holotype: PC).

Robust, shiny to dull, pale whitish-green plants often in deep turfs. Stems (5–)10–30 mm, simple or forking when sterile, generally simple when fertile.

Leaves erect to erect-spreading, crowded and imbricate, lanceolate, 1.5–2.5 mm long, coarsely serrate near the apices; upper cells linear-rhomboidal, 70–135 μm long, 6–11 μm wide, thin-walled. Paroicous; perichaetial bracts gradually enlarged, to 3.5 mm long. Capsules inclined 10°–100° from vertical, longly cylindric, to ca. 6 mm long; exothecial cells elongate-rectangular, 40–80 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows; opercula conic; exostome yellow to red-brown, acute-triangular, bordered, trabeculate; endostome hyaline; basal membrane ½ the height of exostome teeth; segments keeled, broadly to narrowly perforate; cilia long to short, sometimes nodulose. Spores 19–25 μm, rather coarsely papillose. Fig. 7.

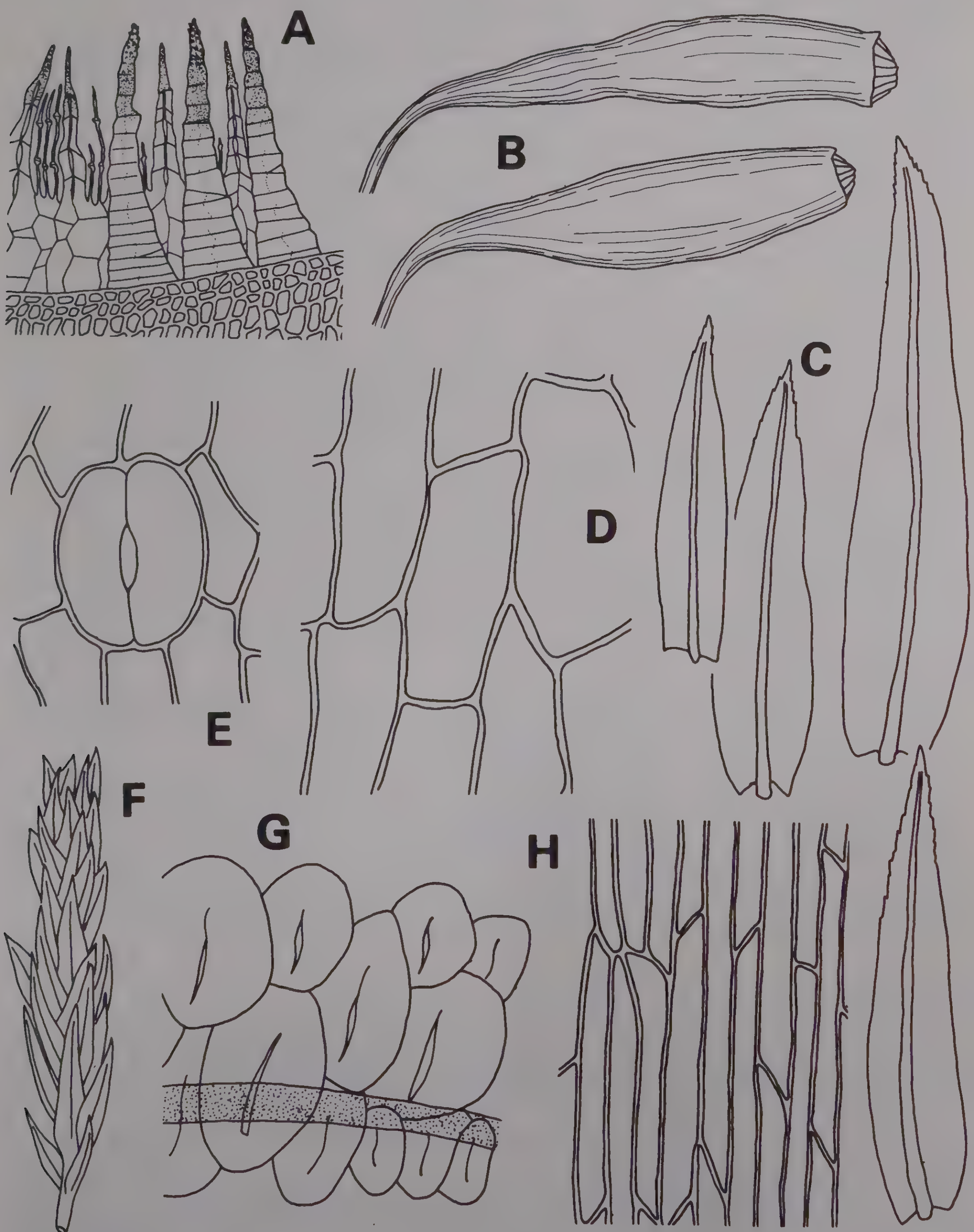


FIG. 7. *Pohlia oerstediana.* A. Peristome, ×80. B. Capsules, ×15. C. Leaves, ×22. D. Exothecial cells, ×290. E. Stomate, ×290. F. Habit, ×4. G. Annulus, ×290. H. Upper leaf cells, ×290.

Soil, moist rocks, tree bark, rotting logs, at high elevations in Oak-Pine forests. Mexico (Hidalgo, Mexico, Oaxaca, Puebla, Tlaxcala, Veracruz). Guatemala (San Marcos, Huehuetenango) and Costa Rica (Volcán Irazu). Map 6.

Exsiccati: Pringle, Plant. Mex. 10548 as *W. cylindrica* (FH).

Pohlia oerstediana is distinguished from *P. cruda* by its larger size, and less glossy leaves that are coarsely serrate near the apex. It is exceptionally robust in microscopic details as well as overall habit (Fig. 7). This species seems to be more common than *P. cruda* in Mexico and Central America, with *P. cruda* more or less restricted to alpine habitats. Most or all records of *P. cruda* given by Bartram (1949) should be referred to *P. oerstediana.*

I have seen few capsules of *P. oerstediana* with intact peristomes, but the segments seem to be variable with respect to perforation. The Asian *Webera laticuspis* Broth. is very similar to *P. oerstediana* gametophytically and has narrowly perforate segments. Such a disjunction, though interesting, is not unheard of among mosses (e.g. *Aoengstroemia orientalis* Mitt.).

6. **Pohlia bolanderi** (Sull.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.
Bryum bolanderi Sull., Mem. Calif. Acad. Sci. 1. 22: 1868.(Lectotype: NY).

Slender to medium-size, glossy green plants in compact turfs. Stems 3–10 (–20) mm, simple or forking when sterile, simple when fertile. Leaves erect to erect-spreading, crowded and imbricate, lanceolate, 1.0–1.6 mm long, serrate to serrulate at the apices; upper cells linear-rhomboidal, 55–100 μm long, 6–9 μm wide, thin-walled. Dioicous; perichaetial bracts scarcely differentiated, to 2 mm long; perigonial bracts shortly acute, erect. Capsules inclined 35°–90° from vertical, elongate-cylindric, 3–5 mm long; exothecial cells elongate-rectangular, 40–85 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, acute; exostome teeth yellow to yellow-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ⅓–½ the exostome length; segments keeled but narrowly perforate; cilia short, rarely long. Spores 16–26 μm, distinctly roughened. Fig. 8.

Rather dry alpine or subalpine soil, less commonly along streams, high montane to alpine. Apparently endemic to western North America; British Columbia; Washington, Oregon, California, Nevada. Map 7.

In addition to the dioicous inflorescence, *P. bolanderi* is distinguished from its close relative, *P. longicollis,* by the smaller overall size and less coarsely serrate leaves. The distinctive geographic range of *P. bolanderi* gives meaning to these relatively slight morphological differences. The distributions of the two species overlap only in southern British Columbia. Reports of *P. longicollis* from California, Oregon, and Washington are referable to *P. bolanderi.*

6a. **Pohlia bolanderi** var. **seriata**, Shaw, var. nov.

Plantae erectae, strictae, dense confertae, plerumque steriles. Folia pallida, dense seriata, imbricata, lanceolata, carinata. Flores dioici. Perichaetia parva, inconspicua, bracteis paucis.

Dull, whitish plants often in deep, luxuriant turfs. Stems erect, up to 5.0 cm high. Leaves ± distinctly arranged in 4–5 vertical rows, pale green to whitish, erect to erect-spreading. Dioicous; perichaetia terminal on simple stems, inconspicuous, the bracts not differentiated from lower leaves. Perigonia and sporophytes as in the var. *bolanderi.* Fig. 9.

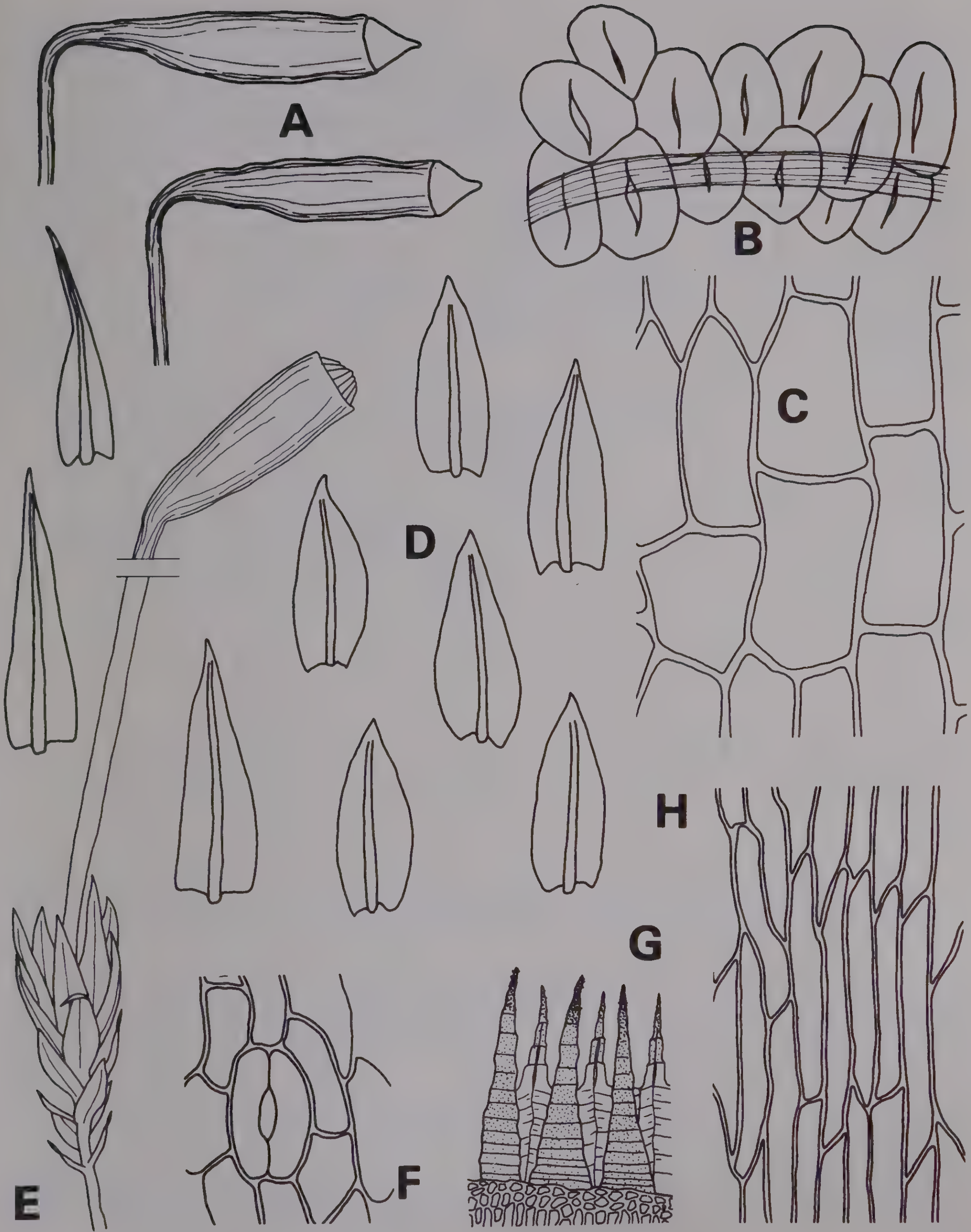


FIG. 8. *Pohlia bolanderi*. A. Capsules, ×15. B. Annulus, ×290. C. Exothecial cells, ×290. D. Leaves, ×22. E. Habit, ×9. F. Stomate, ×290. G. Peristome, ×80. H. Upper cells, ×290.

TYPE: U.S.A. Colorado, Gilpin Co.: 5 mi. E of Corona Pass on Corona Pass Rd., *Shaw 2628* (Holotype: MICH; Isotype: J. Shaw). Paratypes: Colorado, Garfield Co: 30 mi. N of Glenwood Springs, *Hermann 24272* (COLO). Washington, Pierce Co.: Mt. Rainier Nat. P., above Paradise Pt., *Shaw 2453* (J. Shaw).

Moist snowmelt areas in the alpine zone. Colorado, Utah, Wyoming, Washington. Map 7.

The var. *seriata* differs from the var. *bolanderi* in its luxuriant growth and extremely pale leaves often arranged more or less distinctly in vertical rows. At their extremes, the two varieties are very distinct, although several collections

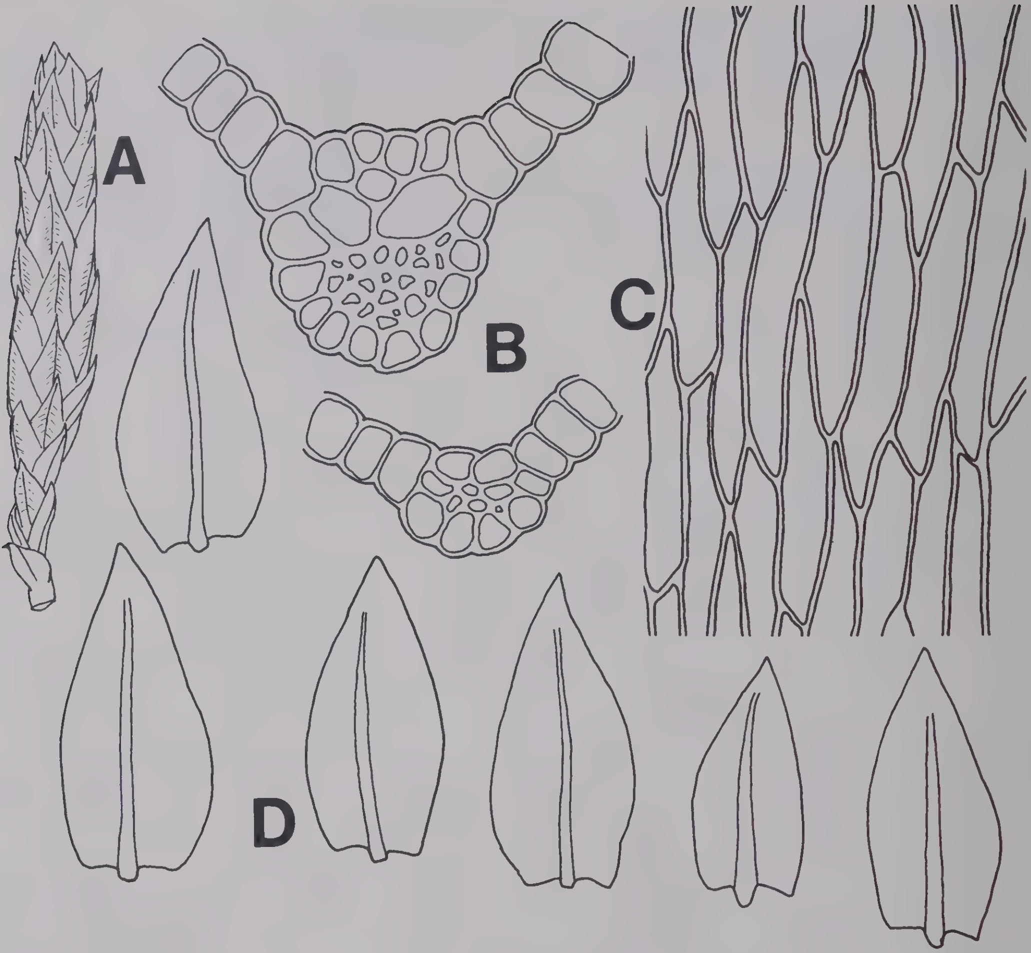


FIG. 9. *Pohlia bolanderi* var. *seriata.* A. Habit, ×35. B. Costae, transverse sections near the leaf base (above) and apex (below), ×290. C. Upper leaf cells, ×290. D. Leaves, ×35.

show intergradation (e.g. *Shaw 2448*, ALTA; *Lawton 2833*, WTU). When well developed, the var. *seriata* looks much like *Conostomum tetragonum* (Hedw.) Lindb. Whereas the var. *bolanderi* is often fertile, I have seen only one specimen of the var. *seriata* with sporophytes (Utah, Cache Co., *Behling 288*, NY). One other collection (*Shaw 2678*, ALTA) has female inflorescences, but all other specimens seen are completely sterile.

Geographic ranges of the two varieties are different, though overlapping (Map 7). The var. *seriata* is characteristic of lush snowmelt areas whereas the var. *bolanderi* grows most frequently on rather dry tundra soil.

7. **Pohlia longicollis** (Hedw.) Lindb., Musci Scand. 18. 1879.

Webera longicollis Hedw., Spec. Musc. 169. 41. f. 1–5. 1801. (Lectotype: G: Hedw.–Schwaegr.).

Bryum longicolle (Hedw.) Sw., Monthl. Rev. 34: 538. 1801.

Hypnum longicolle (Hedw.) Web. & Mohr, Ind. Mus. Pl. Crypt. 3. 1803.

Webera alpina Hoppe & Hornsch. *ex* Hornsch., Flora 2: 104. 1819. (Lectotype: GZU–Hoppe; Isotype: G: Hedw–Schwaegr.).

Bryum grimsulanum Brid., Bryol. Univ. 1: 628. 1826. (Lectotype: B–Brid.; Isotype: G: Hedw.–Schwaegr.).

Mnium crudum var. *longicolle* (Hedw.) Wahlenb., Fl. Suec. 2: 725. 1826.

Webera grimsulana (Brid.) Brid., Bryol. Univ. 2: 829. 1827.

Bryum hornschuchii Spreng., Syst. Veg. 4: 212. 1827 (*nom. illeg. incl. sp. prior.—W. alpina, W. grimsulana*).

Webera longicollis var. *alpina* (Hoppe & Hornsch. *ex* Hornsch.) Fuernr., Flora 12(Ergbl. 2): 36. 1829.

W. longicollis var. *grimsulana* (Brid.) Fuernr., Flora 12(Ergbl. 2): 36. 1829.

Bryum elongatum var. *alpinum* (Hoppe & Hornsch. *ex* Hornsch.) B. & S. *in* B. S. G., Bryol. Eur. 4: 102. 1839.

Pohlia clavata Sendtn., Flora 23: 61. 1840 (*hom. illeg.*; Lectotype: M).

Bryum lucidum Jam. *in* Durand, J. Ac. Nat. Sc. Philadelphia ser. 2, 3: 202. 1856. (Lectotype: FH).

Lamprophyllum longicolle (Hedw.) Lindb., Act. Soc. Sc. Fenn. 10: 26. 1871.

Bryum nitens Kindb., Bih. K. Svensk. Vet. Ak. 7: 66. 1883 (*hom. illeg.*; Lectotype: S–Kindb.).

B. elongatum ssp. *longicolle* (Hedw.) Kindb., Bih. K. Svensk Vet. Ak. Handl. 7: 66. 1883.

B. nitescens Kindb., Bot. Not. 196 (based on *B. nitens*).

Webera pennina De Not. *ex* Par., Ind. Bryol. 1353. 1898 (*nom. nud. in synon.—W. longicollis*).

W. elongata var. *alpina* (Hoppe & Hornsch. *ex* Hornsch.) Herib., Mem. Ac. Sc. Clermont-Ferrand ser. 2, 14: 310. 1899.

Pohlia longicollis var. *alpina* (Hoppe & Hornsch. *ex* Hornsch.) Williams, Bull. New York Bot. Gard. 2: 364. 1902.

Webera nitescens (Kindb.) Kindb. *ex* Macoun, Cat. Canad. Pl. 7: 246. 1902.

Pohlia longicollis var. *grimsulana* (Brid.) Amann, Fl. Mousse. Suisse 2: 179. 1919.

Robust, shiny green plants frequently forming small populations in rock crevices. Stems 8–30 mm, generally simple though sometimes forking. Leaves erect to erect-spreading, crowded and imbricate, lanceolate, acute to acuminate, 1.5–2.6 mm long, coarsely serrate near the apices; upper cells linear rhomboidal, 80–140 μm long, 6–9 μm wide, thin-walled. Paroicous; perichaetial bracts gradually differentiated from lower leaves, to 3.8 mm. Capsules inclined 10°–90° from vertical, elongate-cylindric, 4–6 mm long; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula conic, blunt to acute; exostome teeth yellow to brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ⅓–½ the exostome length; segments keeled but narrowly perforate; cilia short, rarely long. Spores 16–23 μm, distinctly roughened. Fig. 10.

Soil of roadbanks and streambanks, frequently in rock crevices with *P. crudoides* at high latitudes. Circumboreal; across northern North America south in the Rockies to Colorado and in the Appalachians to Tennessee and North Carolina; absent from the Cascade-Sierra Nevada systems. Japan; India; recently reported from East Africa (Mt. Kenya). Map 8.

Exsiccati: Bauer, Musci Eur. Exs. 908 as *W. longicolla* (BH, COLO); Drummond, Musci Amer. 270 as *B. elongatum* (CANM, MICH, NY); Grout, N. Am. Musci Perf. 398 as *P. elongata* (CAS, COLO); Hartmann, Bryac. Scand. Exs. 164 as *W. longicolla* (BH, COLO); Mougeot & Nestler, Stirpes Crypt. 1409 as *W. longicolla* (BH, CANM); Rabenhorst, Bryoth. Eur. 359 as *W. longicolla* (NY, UC), 873 as *W. longicolla* (NY).

Characterized by its large size, glossy, crowded leaves, and paroicous inflorescences, *P. longicollis* is strikingly beautiful. Like *P. elongata* and *P. bolanderi*, *P. longicollis* has the endostome segments narrowly (or scarcely) perforate.

8. **Pohlia polycarpa** (Mitt.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

Bryum polycarpum Mitt., Linn. Soc. Bot. 12: 293. 1869. (Lectotype: NY).

Webera polycarpa (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 134. 1875.

Bryum aggregatum C. Müll., Bull. Herb. Boiss. 5: 181. 1897. (Lectotype: BM–Hampe).

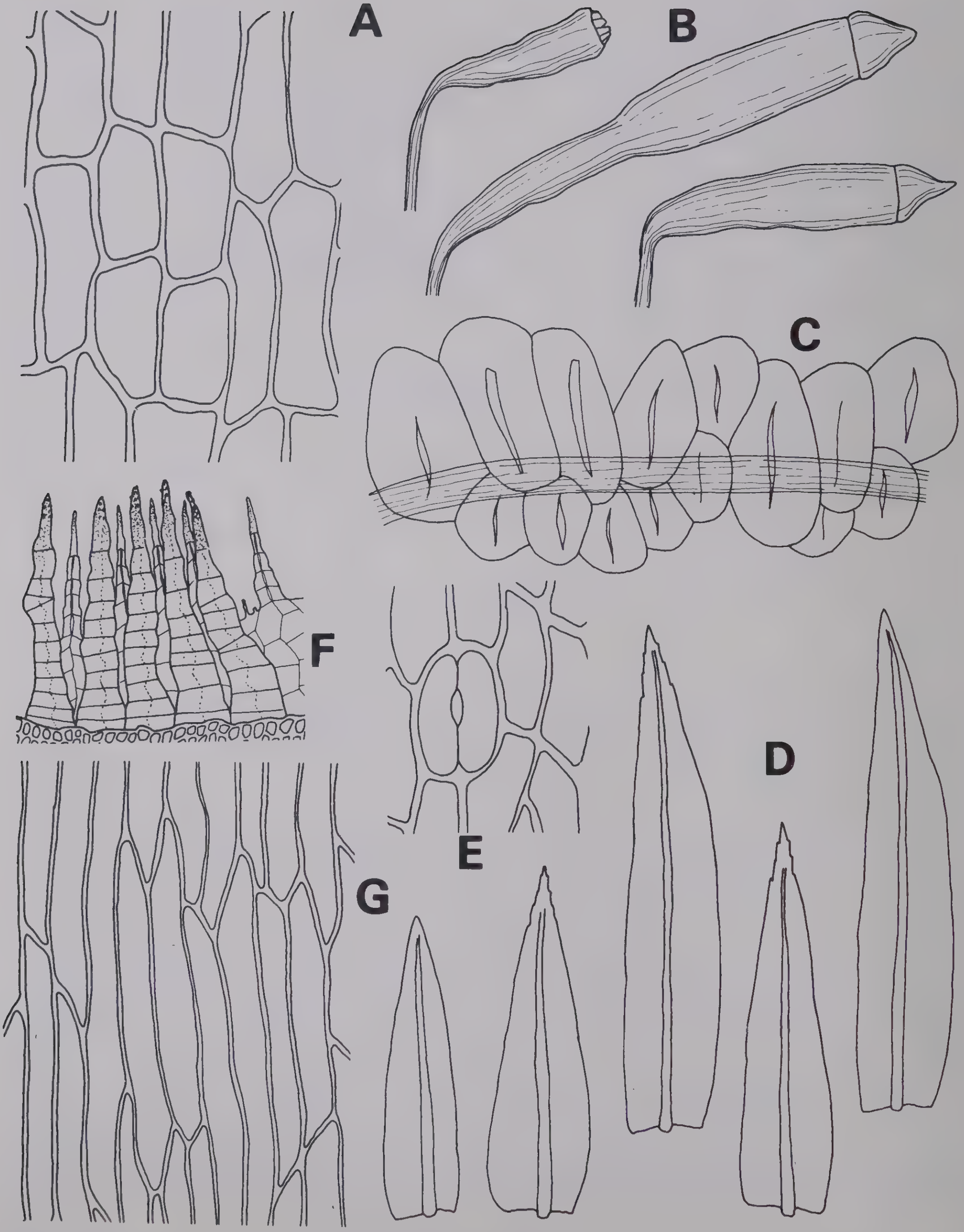


FIG. 10. *Pohlia longicollis.* A. Exothecial cells, ×290. B. Capsules, ×15. C. Annulus, ×290. D. Leaves, ×22. E. Stomate, ×290. F. Peristome, ×80. G. Upper leaf cells, ×290.

Webera aggregata (C. Müll.) Par., Ind. Bryol. 1343. 1898.

Pohlia aggregata (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

P. pluriseta Herz., Beih. Bot. Centralbl. 26: 71. 14. 1910. (Lectotype: JE).

Slender to tiny, glossy green plants forming low turfs. Stems 3–10 mm high, generally simple when sterile, branching by 1–3 innovations below the perichaetia, simple or with a subfloral innovation when bearing perigonia. Leaves erect to erect-spreading, crowded and imbricate, lanceolate, 0.7–1.4 mm long, serrate to serrulate at the apices; upper cells linear-rhomboidal, 50–95 μm long, thin-walled. Dioicous; perichaetial leaves lanceolate to linear-lanceolate, scarcely differentiated or gradually longer than the lower leaves, to 2.5 mm; perigonial bracts shortly acute, erect to erect-spreading. Capsules inclined 10°–95° from vertical, narrowly cylindric, 2.5–4 mm long, 1–4 per perichaetium; exothecial cells elongate-rectangular, 50–90 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula convex to conic, apiculate; exostome teeth yellow-brown to brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline to very pale yellow; basal membrane ca. ⅓ the exostome length; segments weakly to strongly keeled, not or scarcely perforate; cilia rudimentary to absent. Spores 16–20 μm, very finely roughened. Fig. 11.

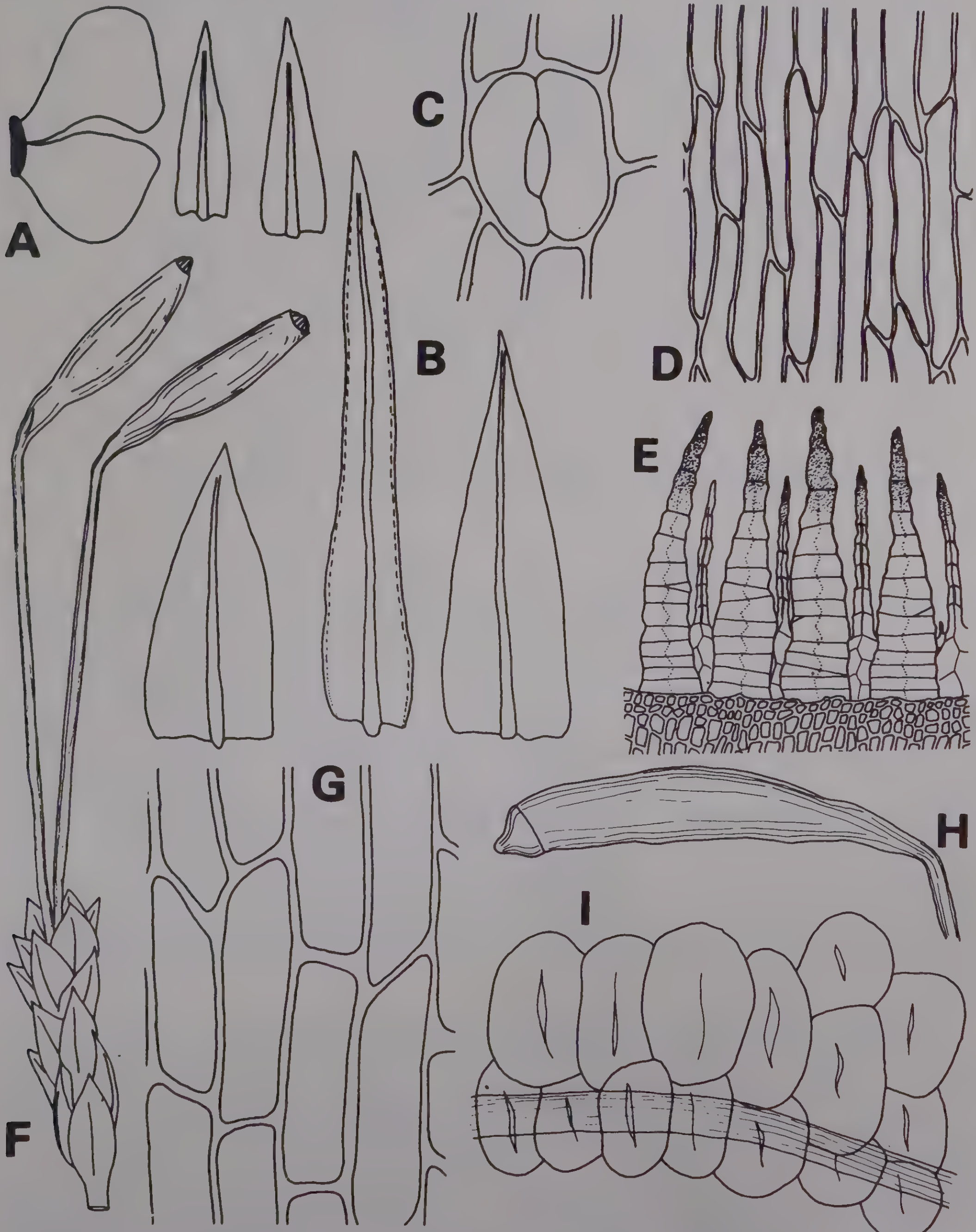


FIG. 11. *Pohlia polycarpa*. A. Lateral view of annular cells, ×290. B. Leaves, including a long perichaetial bract with recurved margins, ×22. C. Stomate, ×290. D. Upper leaf cells, ×290. E. Peristome, ×80. F. Habit, ×8. G. Exothecial cells, ×290. H. Capsule, ×15. I. Annulus, ×290.

On alpine soil; Guatemala (Volcán del Fuego—type, Tajumulco); Bolivia; Peru, Chile. Map 9.

An Andean species, *P. polycarpa* is known in Central ~~America from~~ only two localities in Guatemala. Distinguished at once from related species by the polysetous condition, *P. polycarpa* is otherwise very similar to the northern *P. bolanderi*. *Webera costesii* Card. & Thér. is synonymous with *P. polycarpa* according to a note in the New York Botanical Garden written by Thériot.

9. **Pohlia obtusifolia** (Brid.) L. Koch, Leafl. West. Bot. 6: 20. 1950.

Bryum obtusifolium Brid., Musc. Rec. 2(3): 52. 1803 (type not seen).

Bryum cucullatum Schwaegr., Spec. Musc. Suppl. 1(2): 94. 68. 1816.

Pohlia cucullata (Schwaegr.) Bruch *ex* Hochstetter, Flora 1: 274. 1826.

Bryum vogesiacum Dub. *in* Cand., Bot. Gall. 2: 552. 1830. (Lectotype: RO).

Webera cucullata (Schwaegr.) Schimp., Coroll. 66. 1856.

W. cucullata var. *hausmannii* De Not., Atti Univ. Genova 1: 430. 1869. (Lectotype: RO).

Lamprophyllum cucullatm (Schwaegr.) Lindb., Act. Soc. Sc. Fenn. 10: 87. 1871.

Pohlia cucullata (Schwaegr.) Lindb., Musci Scand. 19. 1879.

Webera microcaulon C. Müll. & Kindb. *in* Macoun, Cat. Canad. Pl. 6: 114. 1892. (Lectotype: S–Kindb.).

W. polymorphoides Kindb. *in* Macoun, Cat. Canad. Pl. 6: 111. 1892. (Lectotype: S–Kindb.).

Pohlia polymorphoides (Kindb. *in* Macoun) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 548. 1903.

Bryum obrutum Stirt. *ex* Dix., J. Bot. 61: 71. 1923 (*nom. nud. in synon.—P. cucullata*).

Bryum oxoniense Dix., Bryol. 32: 2. 1929. (Lectotype BM–Dix; Isotype: BH).

Pohlia serrulata Bruch *ex* Podp., Consp. 337. 1954 (*nom. nud. in synon.—P. cucullata*).

Very small to elongate, pale-green to blackish, rather dull plants in low to deep turfs. Stems 3–8(–25) mm high, simple or rarely forking when sterile, simple or rarely with 1–4 innovations when fertile. Leaves spreading to erect, crowded to distant, broadly lanceolate, broadly acute, subtly cucullate, 0.7–1.4 mm long, serrulate to serrate at the apices; upper cells broadly rhombic, 30–55(–70) μm long, 12–16(–20) μm wide, lax and thin-walled. Paroicous; perichaetial bracts scarcely to moderately differentiated, to 2.8 mm long. Capsules 160°–180° from vertical, broadly pyriform, 2.0–3.5 mm long; exothecial cells elongate-rectangular, 40–75 μm long, with straight walls; stomates superficial; annuli of 2–3 cell rows, revoluble; opercula blunt or umbonate, rarely acute-conic; exostome teeth slenderly triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane low, up to ⅓ the exostome length; segments ± keeled but narrow and delicate, rather broadly perforate; cilia rudimentary to absent. Spores 17–25 μm, distinctly roughened. Fig. 12.

On soil, typically in the alpine zone, frequent in moist, rich snowmelt areas. Circumboreal; in North America known from Alaska, Yukon Territory, Northwest Territories, British Columbia, Alberta, Washington, California, Montana, Wyoming, Colorado; Utah, Labrador, Newfoundland, Quebec, Vermont; India; Japan. Map 10.

Exsiccati: Bauer, Musci Eur. et Amer. Exs. 1925 as *P. cucullata* (CANM), Musci Eur. exs. 312 as *P. cucullata* (BH); Erbar, Crittogam Ital. 1012 as *W. cucullata* (NY, UC); Husnot, Musci Gall. 462 as *W. ludwigii* (BH, NY); Lisowski, Bryoth. Polon. 613 as *P. cucullata* (CANM); Macoun, Can. Musci 468 as *W. cucullata* (NY), 636 a *W. polymorphoides* (NY); Mougeot & Nestler, Stirpes Cryptog. 830 as *P. cucullata* (CANM, NY); Rabenhorst, Bryoth. Eur. 442 as *W. cucullata* (NY); 1215 as *W. ludwigii* (NY);

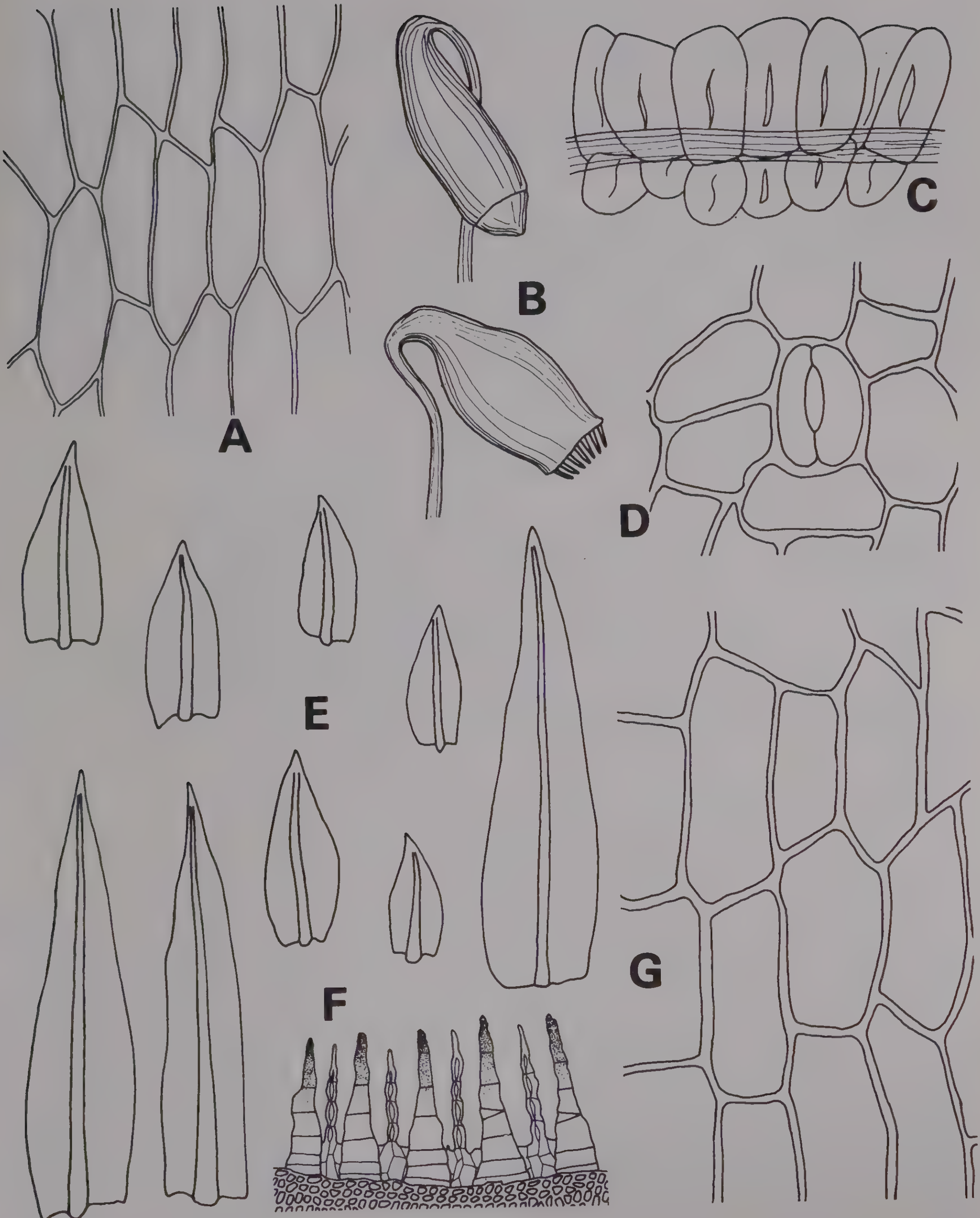


FIG. 12. *Pohlia obtusifolia*. A. Upper leaf cells, ×290. B. Capsules, ×15. C. Annulus, ×290. D. Stomate, ×290. E. Leaves, ×22. F. Peristome, ×80. G. Exothecial cells, ×290.

Sull. & Lesq., Musci Bor. Am. (ed. 1) 176 as *B. cucullatum* (MICH, NY), (ed. 2) 265 as *B. cucullatum* (BH, MICH, NY).

Pohlia obtusifolia is readily distinguished from other species by a combination of gametophytic and sporophytic attributes: paroicous inflorescence, lax, thin-walled leaf cells, and the delicate endostome segments which, although poorly developed, are broadly perforate.

Fruiting plants are typically very small (3–6 mm high), but sterile forms growing in unusually moist sites can reach 2–4 cm. Such forms rarely even produce gametangia, and are most reliably identified by the subtly cucullate leaves and broad cells (12–13 μm or more wide). It is characteristic of elongate expressions to be almost black except for the apical few leaves which are pale-green.

Pohlia obtusifolia is not obviously related to any other North or Central American *Pohlia.* The non-sinuose exothecial cells and revoluble annuli indicate a possible relationship to the previous eight species, but the endostome is more similar to that of *P. cardotii.*

In spite of extensive inquiries to European and North American herbaria, I have been unable to typify *P. obtusifolia*. However, I accept the name rather than using the slightly later *P. cucullata* primarily because after Schwaegrichen described *Bryum cucullatum* in 1816, he noted (1830) that his species was synonymous with Bridel's *Bryum obtusifolium.* Unfortunately, there is no specimen of *B. obtusifolium* in Schwaegrichen's herbarium.

10. **Pohlia crudoides** (Sull. & Lesq.) Broth. *in* Engler & Prantl, Nat Pfl. 1(3): 548. 1903.

Bryum crudoides Sull. & Lesq., Proc. Am. Ac. Arts & Sc. 4: 278. 1859. (Isotype: NY–Mitt.).

Webera crudoides (Sull. & Lesq.) Jaeg., Ber. S. Gall. Naturw. Ges. 1877–78: 440. 1879.

Pohlia crassinervis Lindb., Bot. Centralb. 6: 363. 1881. (Lectotype: H–SOL).

P. crassidens Lindb., Rev. Bryol. 10: 5. 1883. (Lectotype: H–SOL).

Webera trachydontea San., Bot. Centralbl. 13: 247. 1883. (Lectotype: H–SOL).

Bryum crassidens (Lindb.) Kindb., Bih. K. Svensk. Vet. Ak. Handl. 7: 66. 1883.

Webera crassidens (Lindb.) Kindb., Forh. Vid. Selsk. Christiania 1886: 22. 1888.

W. crassinervis (Lindb.) Par., Ind. Bryol. 1343. 1898.

Bryum trachydonteum (San.) C. Müll., Gen. Musc. Fr. 220. 1901.

Medium size to robust, somewhat glossy plants frequently forming small populations in rock crevices. Stems 4–10(–25) mm, deep cherry-red, generally simple but sometimes forking near the base when sterile. Leaves erect-spreading to erect, rather distant, narrowly or rarely broadly lanceolate, acute, 1.0–2.2 (–2.6) mm long, serrate to serrulate at the apices; with strongly recurved margins; upper cells linear-hexagonal, 35–60(–85) μm long, with thin walls. Dioicous; perichaetial bracts lanceolate to linear lanceolate, to 3 mm long; perigonial bracts shortly to longly acuminate, erect to erect-spreading. Capsules inclined 30°–90° from vertical, ovoid-cylindrical, 2.5–4 mm long; exothecial cells shortly to longly rectangular, 30–80 μm long, with straight to weakly sinuose walls; stomates superficial; annuli of 2–3 cell rows, revoluble or separating irregularly; opercula convex to conic, acutely to bluntly apiculate; exostome teeth whitish to yellow, slenderly triangular, rounded at the apex, coarsely papillose throughout, scarcely bordered, weakly trabeculate; endostome whitish to hyaline; segments narrow and scarcely keeled, very narrowly perforate to entire; basal membrane low, to ⅓ the exostome length; cilia absent or rarely rudimentary. Spores 15–25 μm, finely roughened. Fig. 13.

On soil especially in rock crevices in tundra habitats; according to Ochi (1959), on soil also in the deciduous zone of Japan (as var. *revolvens*). Alaska, Yukon Territory, Northwest Territories and British Columbia; Greenland; northern Europe and Asia; Japan; India. Map 11.

Exsiccati: Noguchi, Musci Jap. 936 as *P. crudoides* (CANM, NY); Savicz-Lubitzkaja, Hep. et Musci U.R.S.S. Exs. 96 as *P.crudoides* (CANM, CAS).

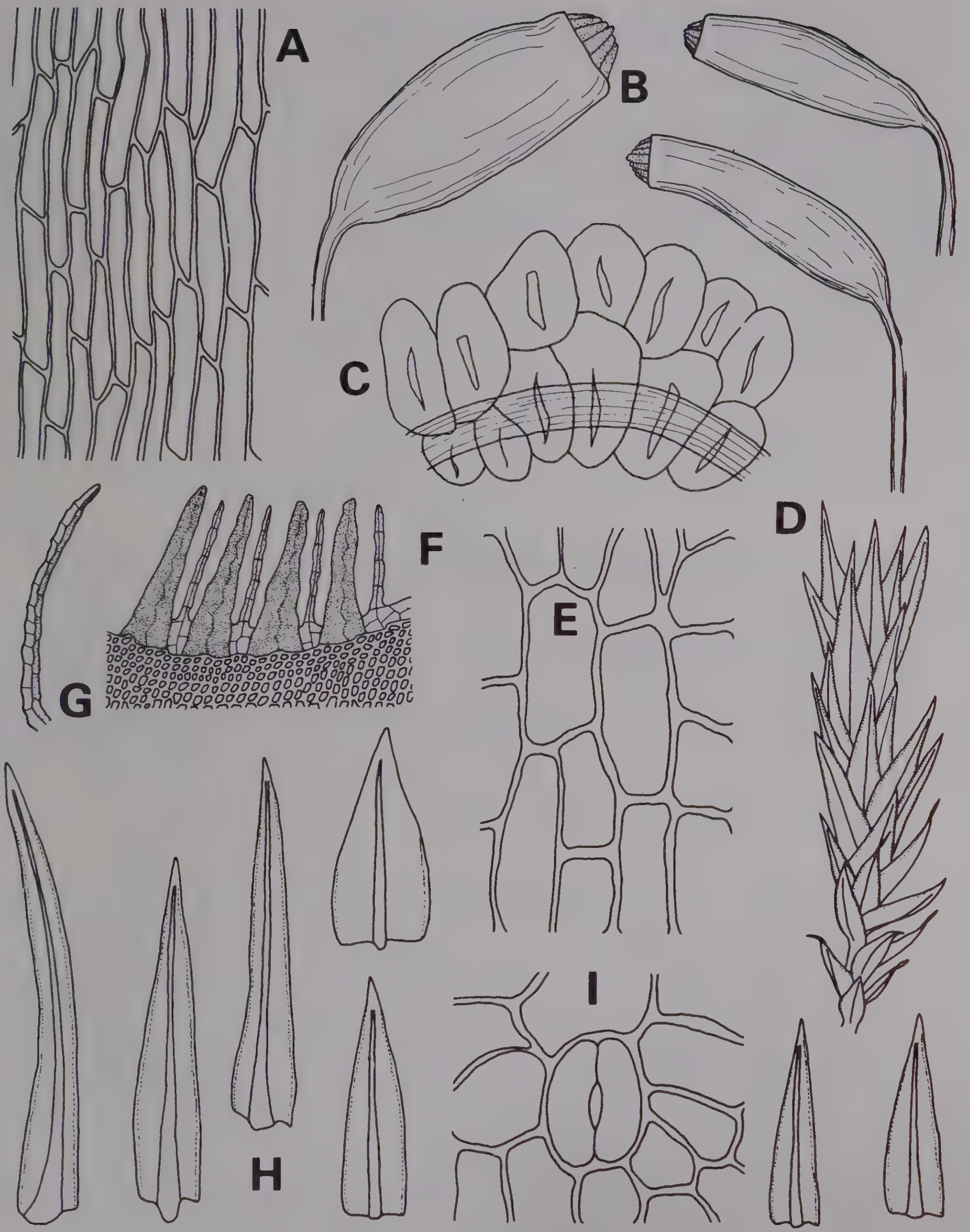


FIG. 13. *Pohlia crudoides*. A. Upper leaf cells, ×290. B. Capsules, ×15. C. Annulus, ×290. D. Habit, ×4. E. Exothecial cells, ×290. F. Peristome, ×80. G. Lateral view of exostome tooth showing weakly developed trabecula, ×80. H. Leaves, perichaetial bracts on the leaf, ×22. I. Stomate, ×290.

Pohlia crudoides can be recognized by cherry-red stems and obviously recurved leaf margins. The leaves are generally long, narrow and somewhat stiff, although I have seen a few sterile plants from the Yukon Territory with broader, less stiff leaves and hardly recurved margins. *Pohlia crassinervis* Lindb. typifies such expressions, which do not seem to justify separation.

Pohlia crassidens Lindb. and *Webera trachydontea* San. are based on the same type specimen (collected in Opdal by Kaurin). There is no specimen representing *W. trachydontea* in the Sanio herbarium (Rusińka *in litt*, 1979). To avoid future ambiguity, I have chosen a single specimen in Lindberg's herbarium to lectotypify both names. The Himalayan type of *Webera timmioides* Broth. is close to *P. crudoides*, distinguishable solely by its very robust stature. Both syntypes lack sporophytes.

11. **Pohlia papillosa** (C. Müll. *ex* Jaeg.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Bryum papillosum C. Müll., Syn. 1: 326. 1848. (Lectotype: NY; Isotype BM–Besch.). *hom. illeg.—non B. papillosum* Dicks.

B. tenellum Schimp. *ex* C. Müll., Syn. 2: 572. 1851. (Lectotype: BM–Schimp.; Isotype: NY).

Brachymenium tenellum (Schimp. *ex* C. Müll.) Schimp. *ex* Besch., Mém. Soc. Sc. Nat. Cherbourg 16: 195. 1872.

B. papillosum (C. Müll. *ex* Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 122. 1875.

B. subglobosum Schimp. *ex* Besch., Ann. Sci. Nat. Bot. ser. 6, 3: 204. 1876. (Lectotype: BM–Besch.; Isosyntype: NY, BM–Hampe).

Bryum mammillosum C. Müll., Bull. Herb. Boiss. 5: 550. 1897. (Lectotype: NY).

Brachymenium mammillosum (C. Müll.) Par., Ind. Bryol. Suppl. 39. 1900.

Pohlia mammillosa (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Pohlia subglobosa (Schimp. *ex* Besch.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Webera papillosa (C. Müll. *ex* Jaeg.) Herz., Biblioth. Bot. 87: 79. 1916.

W. mammillosa (C. Müll.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 362. 1924.

W. subglobosa (Schimp. *ex* Besch.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 362. 1924.

Medium-sized dull green plants sometimes forming extensive turfs. Stems 5–25 mm, simple or commonly forking when sterile, with 1–4 innovations below the perichaetia, simple when bearing perigonia. Leaves erect-spreading, frequently distant on sterile stems, crowded when fertile, lanceolate, 0.7–1.4 mm long, serrate to serrulate at the apices; upper cells rhomboidal, 60–90(–110) μm long, 6–9 μm wide, with firm walls. Gemmae numerous in the upper leaf axils, arising in clusters in each axil, linear-vermicular, oblong, or obconic, 100–250 μm long but apparently indeterminate in growth, brown or whitish, pink or reddish, with 1–4 peglike, erect, leaf primordia at the apex, the primordia sometimes 2–3 cells broad at the base. Dioicous; perichaetial bracts linear-lanceolate, to 3.0 mm long; perigonial bracts erect-spreading. Capsules inclined 10°–100° from vertical, broadly to narrowly pyriform, narrowed at the mouth, sometimes curved and slightly asymmetric, 2.5–4.0 mm long; exothecial cells isodiametric to shortly rectangular, 35–60 μm long, with straight or rarely sinuose, often strongly bulging walls; stomates superficial to somewhat sunken; annuli of 1(2) cell rows, separating irregularly; opercula convex and apiculate or shortly and bluntly rostrate (and sometimes curved upward); exostome teeth whitish to yellow, ± fused near the base; slenderly triangular, ± blunt at the apices, coarsely papillose throughout, scarcely bordered, weakly trabeculate; endostome whitish to hyaline, papillose; segments narrow and scarcely keeled, very narrowly perforate to entire; basal membrane low, to ⅓ the exostome length; cilia absent or rarely rudimentary. Spores 17–21 μm, finely roughened. Fig. 14–15.

On soil of roadbanks or in other disturbed sites, most frequent at moderate altitudes in cloud forests; Mexico (Chiapas, Chihuahua, Hidalgo, Mexico, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Veracruz); Cuba; Dominican Republic; Haiti; Jamaica; Guatemala; Costa Rica; Panama; Columbia, Venezuela; Peru; Ecuador; Brazil. Map 12.

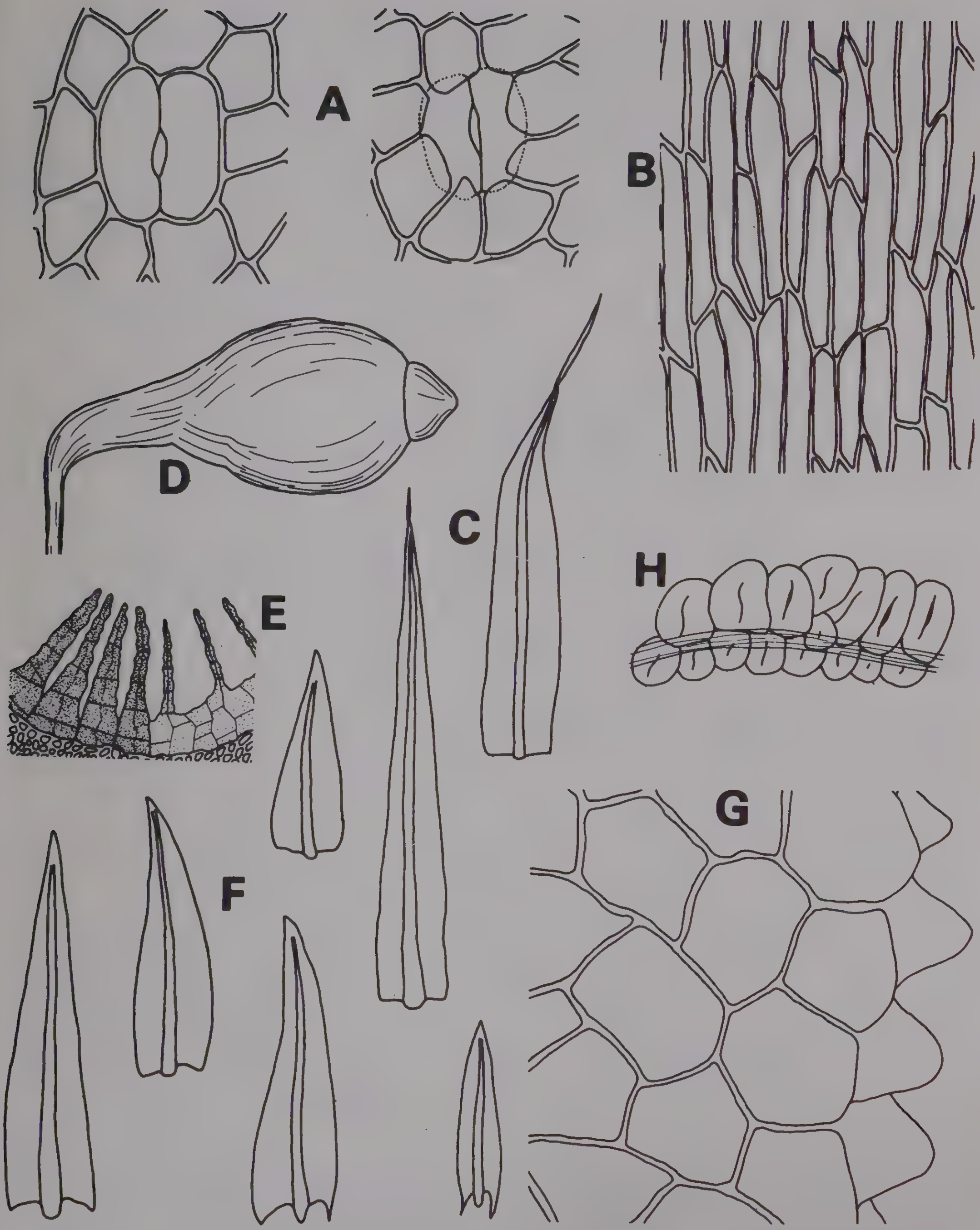


FIG. 14. *Pohlia papillosa*. A. Stomates, ×290. B. Upper leaf cells, ×290. C. Perichaetial bracts, ×22. D. Capsule, ×15. E. Peristome, ×80. F. Leaves, ×22. G. Exothecial cells, ×290. H. Annulus, ×290.

Exsicatti: Pringle, Plantae Mex. 10635 as *W. didymodontia* (MO).

Ecologically, *P. papillosa* replaces *P. annotina* and related species in the Neotropics. It reproduces by axillary gemmae, and is common in disturbed areas. The gemmae are variable in shape, encompassing most of the forms characteristic of *P. proligera* and *P. annotina* combined. They are usually very small (ca. 100 μm) and linear-vermicular with one primordium, but are sometimes obconic with 2–4 peglike (or rarely more or less laminate) primordia. Many specimens have only dense clusters of small vermicular gemmae. Several Mexican collections have very small ovoid gemmae with poorly developed leaf primordia

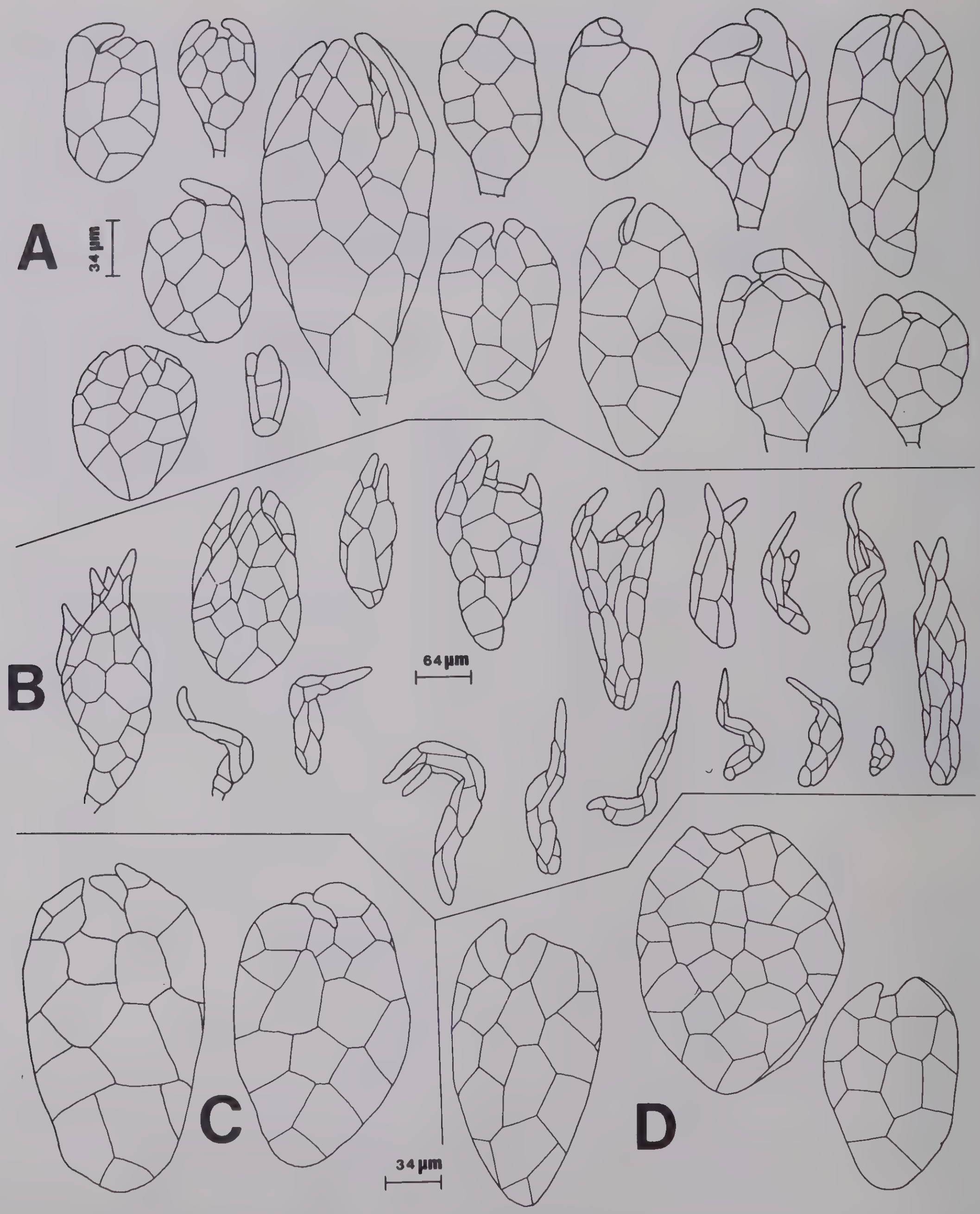


FIG. 15. Gemmae of *Pohlia* and *Bryum* species. A. *Pohlia richardsii*. B. *Pohlia papillosa*. C. *Bryum* sp., *Fife 2827*. D. *Bryum gemmiluscens* Wilz. & Dem., *Dehle*, 1824 (BM).

(e.g. *Bowers et al. 5385; Sharp et al. 1325; Iwatsuki & Sharp 5339b;* all in TENN). These may prove to be poor examples of *P. papillosa*, but require further study.

Contrary to Andrews (1950), I find *P. papillosa* to be consistently distinct from the Old World, *P. flexuosa* Hook. The two are quite similar, but *P. flexuosa* has longly acuminate exostome teeth (370–600 µm vs 240–370 µm in *P. papillosa*), completely separate to the base and segments distinctly keeled and narrowly perforate. The exothecial cells are often only weakly bulging whereas they are strongly so in *P. papillosa*. Gemmae of *P. flexuosa* are often scarce, but are generally linear-obconic to ovoid with 3–5 peglike primordia. I have seen *P. flexuosa* from Japan, the Philippines, China, India, Nepal and Africa (Rwanda), and it is apparently endemic to the Old World.

A number of species have been segregated from *P. flexuosa* on the basis of differences in gemmae form. Andrews (1950) referred *Pohlia delicatula* (Mitt.) Broth. to the synonymy of *P. flexuosa*, but it is a clearly distinct species distinguished by leaf shape and aereolation as well as gemmae morphology. Like the European *P. muyldermansii* Wilz. & Dem., *P. delicatula* has two kinds of gemmae: linear with poorly developed primordia and tiny, isodiametric to ovoid types. Unlike *P. muyldermansii*, the ovoid gemmae do not have protruding walls. The Hawaiian *P. leucostomoides* (Broth.) Bartr. has larger, translucent ovoid gemmae devoid of primordia in the leaf axils.

12. **Pohlia richardsii** Shaw, sp. nov.

Plantae caespitosae vel gregariae. Caules fertiles ramosissimi, breves, steriles plerumque simplices, gemmiferi duplo et triplo longiores, uniformiter foliosi, erecti. Folia lanceolata vel lineali-lanceolata, apice irregulariter serrata, inferne margine reflexa, areolis cellulis superioribus linearibus. Capsulae late pyriformes. Gemmae abundantes, axillis foliorum summorum, intense rubrae, ovoideae.

Dull green plants. Stems 5–15 mm, simple when sterile or bearing antheridia, innovating rather abundantly when bearing archegonia. Leaves erect-spreading to spreading when moist, scarcely altered on drying; 0.7–1.4 mm long, 0.3–0.6 mm wide, lanceolate, acute, somewhat decurrent by 3–4 rows of rectangular cells; margins plane to ± reflexed, serrate to serrulate near the apex or halfway to the base, entire below; costa ending 1–3 cells below the apex; upper cells linear-rhomboidal, (40–)50–80(–95) μm long, 6–9 μm wide, thin- to firm-walled, not or rarely vermicular, undifferentiated along the margin, rectangular near the base. Gemmae numerous to few in upper leaf axils, arising in clusters in each axil, rarely appearing single on older shoots, spheroidal, ovoid, obovoid, or obconic, about 110–160 μm long but apparently indeterminate in growth, deep red to orange-red, with 1–4 short, inconspicuous leaf primordia at the apex, the primordia rarely rudimentary, sometimes peglike, but mostly laminate (3 cells or more broad at the base), incurved over the apex, paler than the body but not green. Dioicous; perigonia bulbiform; outer bracts longly acute to acuminate, erect to erect-spreading from an erect base; perichaetia terminal, rather inconspicuous; outer bracts to ca. 2.2 mm long, triangular- to linear-lanceolate; margins recurved from base to apex. Sporophytes uncommon; setae 10–15 mm high, orange to orange-red; capsules inclined about 90°, 2.5–3.5 mm long, tan to brown, broadly pyriform, abruptly contracted to a well-developed neck; exothecial cells isodiametric to short-rectangular, 35–55 μm long, 18–40 μm wide, with non sinuose but bulging walls; stomates superficial to ± sunken, 35–55 μm long; annuli of 1(2) cell row(s), separating irregularly; opercula bluntly convex to hemispheric; exostome teeth white to yellowish-white, narrowly lanceolate, ± blunt, (200–)220–330(–370) μm long, weakly bordered, hardly trabeculate, densely and rather coarsely papillose from apex to base dorsally; endostome white to hyaline; basal membrane ca. ⅓ the exostome length; segments linear to linear-laneolate, not or slightly keeled, not perforate; cilia none. Spores 10–20 μm, finely papillose to nearly smooth. Fig. 15–16.

TYPE: Costa Rica, Volcán Poas, on banks of volcanic ash near edge of water, c. 2,500 m, 20 Feb. 1965, *Richards R 6010* (Holotype: MICH). Paratypes: Colombia, Dept. Santander: Vicinity of California, 3000 m, *Kilip & Smith* (NY). Dept. Cundinamarca: ca. 1 km S of Usme, ca. 9000 ft., *King et al. C–6000* (US). Ecuador, Prov. Napo: Páramo de Guamami, N of Quito-Baeza Rd., 4200 m, *Steere E–250* (NY). Venezuela, Nova Granada, *Linding* (NY).

On soil. Costa Rica (De Alajuela, San José); Colombia; Venezuela; Ecuador. Recently collected in the Dominican Republic (La Vega, *Shaw 5621*). Map 13.

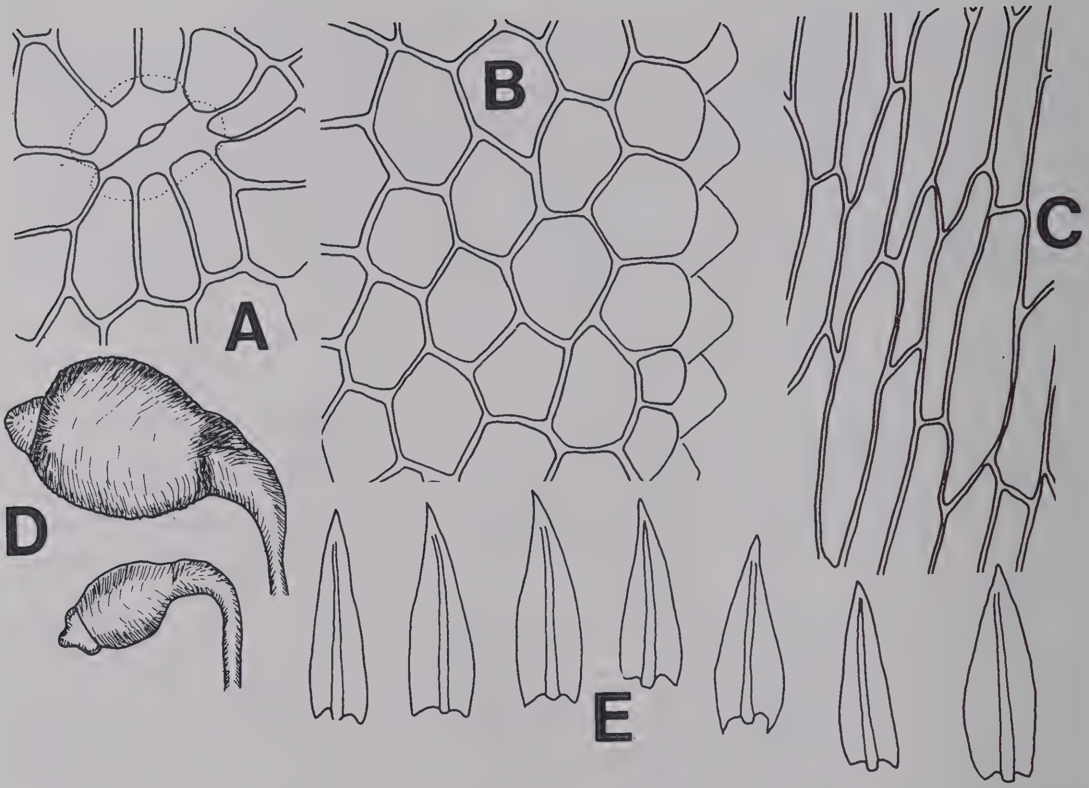


FIG. 16. *Pohlia richardsii.* A. Stomate, ×290. B. Exothecial cells, ×290. C. Upper leaf cells, ×290. D. Capsules, ×15. E. Leaves, ×22.

Pohlia richardsii was collected by Paul Richards in 1965 and was subsequently sent to H. Crum, who recognized it as a new species. I am grateful to them for permission to describe it here.

This is apparently a species of the nothern Andes and Central America, penetrating northward only to Costa Rica, though disjunct in the Dominican Republic. The only fruiting plants of *P. richardsii* available, all collected by D. Griffin and collaborators in Costa Rica, are unfortunatly mixed with *P. papillosa.* I was able to convince myself that at least some of the sporophytes belong to *P. richardsii* gametophytes, although there is nothing to distinguish the capsules from those of *P. papillosa.* This similarity is comparable to the uniformity among capsules of *P. annotina* and related species.

Pohlia richardsii is distinguished from *P. papillosa* by the deep red to orange, spherical to short-oblong gemmae. The only time that *P. papillosa* approaches *P. richardsii* in gemmae form is in very poorly-developed expressions of the former that have few, small gemmae, with rudimentary primordia. In such cases, the gemmae are pale, rather than dark and translucent. Even in mixed specimens of *P. papillosa* and *P. richardsii*, it is possible to separate stems of the two. *Pohlia richardsii* can also be distinguished from such other propaguliferous species as *P. pseudo-barbula* and *Pseudopohlia didymodontia* by smaller gemmae.

Gemmae like those of *P. richardsii* are found in several unrelated species of Bryaceae. For example, *Bryum gemmilucens* Wilz. & Dem. has gemmae practically indistinguishable from those of *P. richardsii* (Fig. 15). Similar forms occur on stems of a sterile and unidentified *Bryum* collected by A. Fife in Newfoundland (Fig. 15), and those of *P. andrewsii* are also similar (Fig. 23).

13. **Pohlia pseudo-barbula** (Thér.) Crum *ex* Shaw, comb. nov.

Webera pseudo-barbula Thér., Smiths. Misc. Coll. 85: 28. 17. 1931. (Lectotype: PC; Isosyntype: F).

Slender dull-green plants. Stems 5–15 mm, generally unbranched when sterile, with 1–4 innovations below the perichaetia, simple when bearing perigonia. Leaves erect to erect-spreading, crowded on the stem, lanceolate, 0.7–1.4 mm long, serrate or serrulate to midleaf or below; upper cells rhomboidal, 50–75(–90) μm long (longer on perichaetial leaves) 6–9 μm wide, with firm walls. Propagula present in clusters in upper leaf axils, ovoid to spherical or obconic, abruptly narrowed to a uniseriate stalk, red to orange, (140–)160–230(–300) μm long, with 2–5 apical and subapical, erect or incurved leaf primordia, the primordia laminate in form (2–5 cells broad at the base). Dioicous; perichaetial bracts lanceolate to linear-lanceolate, to 3.0 mm long; perigonial bracts shortly to longly acuminate, erect-spreading. Capsules inclined 10°–90° from vertical, narrowly pyriform to cylindrical, 2.5–4.0 mm long, slightly curved and asymmetric; exothecial cells longly to shortly rectangular, 35–65 μm long, with somewhat sinuose walls; stomates superficial; annuli of 2 cell rows, separating irregularly; opercula conic, acute or apiculate; exostome hyaline to whitish, narrowly triangular, ± blunt, coarsely papillose in the upper ½, more finely roughened below, scarcely bordered, weakly trabeculate; endostome hyaline; basal membrane low, to ⅓ the exostome length; segments linear but slightly keeled, not or very narrowly perforate; cilia absent or rarely rudimentary. Spores 13–20 μm, nearly smooth or somewhat roughened. Fig. 17.

On soil, especially along roadsides in montane Oak-Pine forests. Apparently endemic to Mexico, where it is known from the volcanic region around Mexico City (Distrito Federal, Hidalgo, Michoacán, Puebla). Map 14.

This species is related to *P. papillosa*, as indicated by the weakly bordered and trabeculate, rather short exostome teeth, linear scarcely keeled, narrowly split segments, and low basal membrane, lacking cilia altogether. Like *P. papillosa*, it reproduces by axillary gemmae. It is distinguished by narrowly cylindrical capsules with rectangular, nonbulging exothecial cells, and far less coarsely papillose exostome teeth that are almost smooth below.

I have examined all four of the syntypes cited by Thériot. The lectotype is an abundant specimen bearing both sporophytes and axillary gemmae. An additional specimen collected by Brother Amable in Cuautzin (no. 1827) was reported by Thériot (1932). A duplicate in the Mitten collection (NY) agrees precisely with the syntypes. Crum (1951) made the combination *Pohlia pseudobarbula* in his thesis, but since that is not considered effective publication, the combination is validated here. The author citation should therefore be *P. pseudobarbula* (Thér.) Crum *ex* Shaw.

14. **Pohlia ludwigii** (Schwaegr.) Broth., Act. Soc. Sc. Fenn. 19: 27. 1892.

Leskea ludwigii [Spreng. *ex*] Web. & Mohr, Ind. Musc. Pl. Crypt. 3: 1803. (*nom. nud.*).

Bryum ludwigii Schwaegr., Spec. Musc. Suppl. 1(2): 95. 68. 1816. (Lectotype: G: Hedw.–Schwaegr.).

Webera ludwigii (Schwaegr.) Fuernr., Flora 12(Ergbl. 2): 35. 1829.

Bryum bigelovii Sull., Rep. Expl. Surv. Rout. Railr. 4: 187. 5. 1856. (Lectotype: FH).

Webera breidleri Jur., Verh. Zool. Bot. Ges. Wien 20: 167. 3b. 1870. (Lectotype: W).

Bryum breidleri (Jur.) Hobk., Grevillea 1: 157. 1873.

Webera bigelovii (Sull.) Lesq. & James, Man. N. Am. Moss. 223. 1884.

Pohlia bigelovii (Sull.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 50. 1903.

Webera ludwigii var. *breidleri* (Jur.) Roth, Eur. Laubm. 2: 26. 1904.

Bryum grande (Kindb.) Par., Ind. Bryol. ed. 2, 1: 217. 1904 (*nom. inval. in synon.—B. ludwigii*).

Mniobryum bigelovii (Sull.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

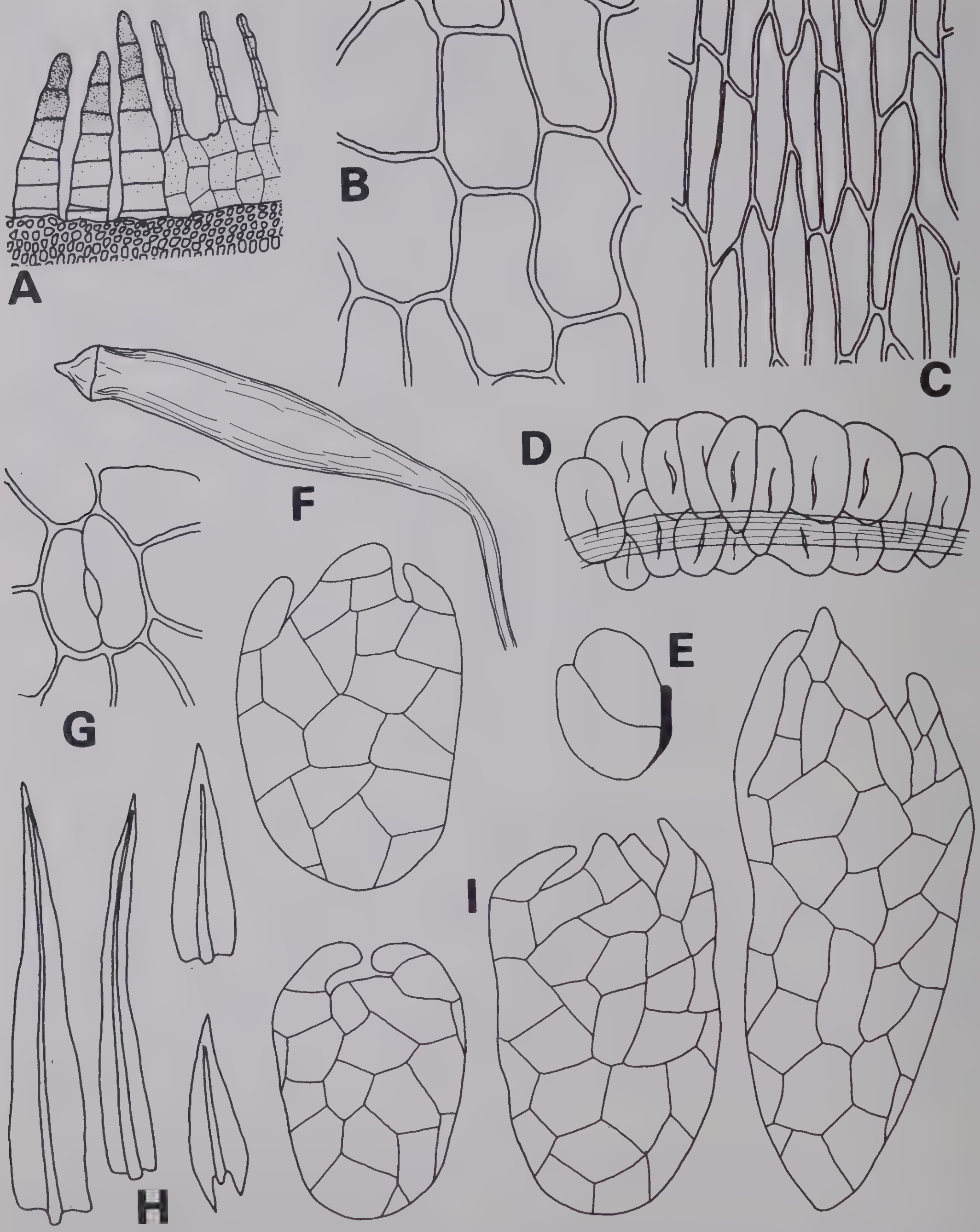


FIG. 17. *Pohlia pseudo-barbula*. A. Peristome, ×80. B. Exothecial cells, ×290. C. Upper leaf cells, ×290. D. Annulus, ×290. E. Lateral view of annular cells, ×290. F. Capsule, ×15. G. Stomate, ×290. H. Leaves, ×22. I. Gemmae, ×180.

M. ludwigii (Schwaegr.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

Pohlia sudetica Podp. *ex* Gyoerffy, Mag. Bot. Lapok 18: 21. 1919 (*nom. illeg. incl. spec. prior.—B. ludwigii*).

P. ludwigii var. *breidleri* (Jur.) Amann. Fl. Mouss. Suisse 2: 182. 1819.

Webera sudetica Giac., Atti Ist. Bot. Univ. Lab. Critt. Pavia Ser. 5, 4: 231. 1947 (*nom. illeg. incl. spec. prior.—B. ludwigii*).

Mostly robust, dull green plants in deep turfs. Stems 8–35 mm, simple or frequently forking when sterile, simple when bearing perichaetia, simple or with 1–3 innovations when bearing perigonia. Leaves spreading to erect-spreading, distant to crowded, ovate-lanceolate, acute to rounded at the apices, 1.5–2.0 (–2.6) mm long, serrate near the apices, ± longly decurrent; upper cells rhombic to rhomboidal, 40–65(–85) μm long, 7–12 μm wide, with firm to rather thin walls. Dioicous; perichaetial bracts lanceolate, not strongly differentiated in shape but with the costa very broad at the base, to 3.2 mm long; perigonial bracts shortly to longly acuminate, erect-spreading. Capsules 90°–180° from vertical, broadly pyriform, 2–3.5 mm long; exothecial cells shortly rectangular, 25–65 μm long, with sinuose walls; stomata superficial; annuli of 2–3 cell rows, separating irregularly; opercula conic, blunt to apiculate; exostome yellow to brown, acute-triangular, most coarsely papillose at the apex, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled and broadly perforate; cilia long, nodulose. Spores 14–21 μm, finely roughened. Fig. 18.

Rare; on soil, especially in arctic or alpine tundra, often in lush snowmelt areas. North America (Alaska, British Columbia, Washington, Montana); northern and central Europe; Japan. Map 15.

Exsiccati: Bauer, Musci Eur. Am. Exs. 2027 as *W. ludwigii* (CANM), Musci Eur. Exs. 1624 as *P. ludwigii* (ALTA, NY), 1625 as *P. ludwigii* f. *adscendens* (ALTA, NY), 1626 as *P. ludwigii* f. *fragilis* (ALTA, NY), 1627a as *P. ludwigii* f. *aquatica* (ALTA, NY), 1627b as *P. ludwigii* f. *erecta* (NY); Husnot, Musci Gall. 520 as *W. ludwigii* v. *major* (BH); Lisowski, Bryoth. Polon. 286 as *P. ludwigii* (CANM).

Pohlia ludwigii is uncommon in North America. It is characteristic of moist, rich snowmelt areas in tundra sites, where it is usually sterile but forms rather deep cushions. Schofield and Tan collected beautiful fruiting plants in British Columbia (*74439*, UBC). According to Schofield (*in litt.*, 1980), capsules are produced late in the season, thus rarely collected. The species is recognized when sterile by the pink color of the lower leaves, and broadly lanceolate, longly decurrent leaves with the apices more or less cucullate (when moist).

Plants collected by Schnooberger (*1382*) and Moxley (1936, 1941) from Bruce Co., Ontario and distributed as *P. ludwigii* are *Bryum gemmiparum* De Not. Collections made by Bartram in Arizona and determined by Andrews as *P. commutata* (= *P. drummondii*) or *P.ludwigii* are also *B. gemmiparum*.

The type of *Bryum bigelovii* Sull. is, by default, an odd expression of *P. ludwigii*. Sporophytically it is more or less typical, but the leaves are not very decurrent and have rather lax, thin-walled cells. It represents the only record of *P. ludwigii* in California (although it is not surprising). The type of *Bryum ludwigii* ssp. *grande* Kindb. is a sterile *Philonotis*. A specimen of *P. ludwigii* in Schwaegrichen's herbarium closely matches his illustration, providing one of few instances where typification is unambiguous!

15. **Pohlia cardotii** (Ren. *in* Ren. & Card.) Broth.*in* Engler & Prantl, Nat. Pfl. 1(3): 547. 1903.

Webera cardotii Ren. *in* Ren. & Card., Rev. Bryol. 15: 71. 1888. (Type not seen).

Bryum commutatum ssp. *cardotii* (Ren. *in* Ren. & Card.) Kindb., Eur. N. Am. Bryin. 2: 388. 1897.

Pohlia porosa H. Lindb., Bull. Torr. Bot. Club 27: 318. 21. 1900. (Lectotype: H; Isotypes: COLO, DUKE, MICH, NY, UBC).

Bryum cardotii (Ren. *in* Ren. & Card.) Kindb. *ex* Par., Ind. Bryol. Suppl. 1900 (*nom. inval. in synon.—W. cardotii*).

Webera porosa (H. Lindb.) Par., Ind., Bryol. ed. 2, 5: 120. 1906.

Medium-sized to robust, dull green plants often forming deep turfs. Stems 3–10(–25) mm high, simple or forking when sterile, simple or rarely innovating below perichaetia, simple when bearing perigonia. Leaves erect to erect-

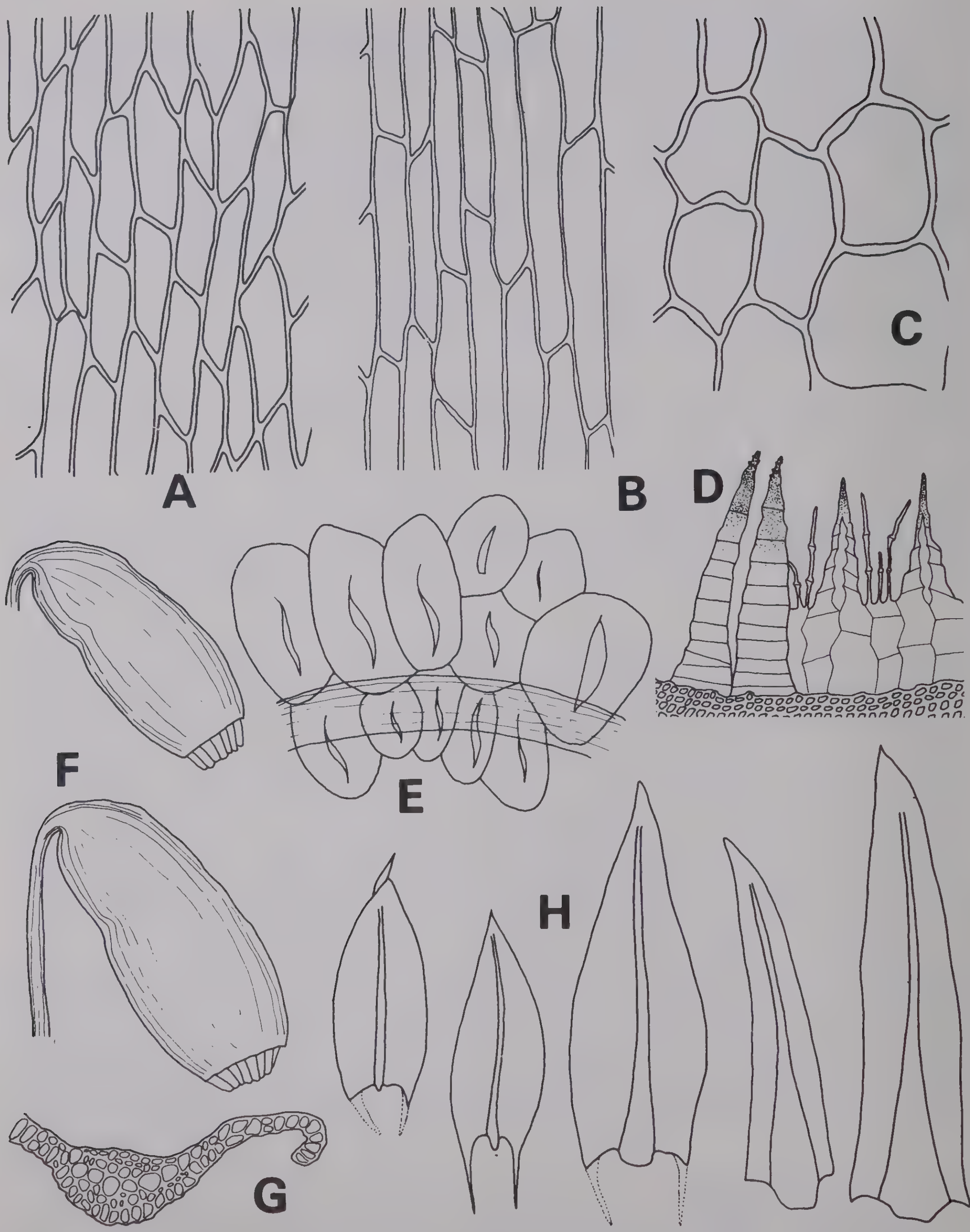


FIG. 18. *Pohlia ludwigii.* A. Upper cells of branch leaf, ×290. B. Upper cells of perichaetial bract, ×290. C. Exothecial cells, ×290. D. Peristome, ×80. E. Annulus, ×290. F. Capsules, ×15. G. Transverse section of perichaetial bract near the base, ×290. H. Leaves, ×22.

spreading, crowded, lanceolate, 0.7–1.5 mm long, serrulate to entire at the apex; costa strong, broad; upper cells rhombic, 18–35(–55) μm long, 6–9 μm wide, with thickened, often porose walls. Dioicous; perichaetial bracts somewhat differentiated, lanceolate to triangular, to 2.6 mm long; perigonial bracts shortly acute, erect. Capsules erect or nearly so, symmetric, narrowly pyriform, 2.0–3.0 mm long; exothecial cells shortly rectangular, 35–55 μm long, with ± strongly sinuose walls; stomates superficial; annuli of 2–4 cell rows, separating irregularly; opercula conic, acute; exostome teeth yellow to brown, ± narrowly triangular, obtuse or ± acute, most coarsely papillose near the apices, bordered,

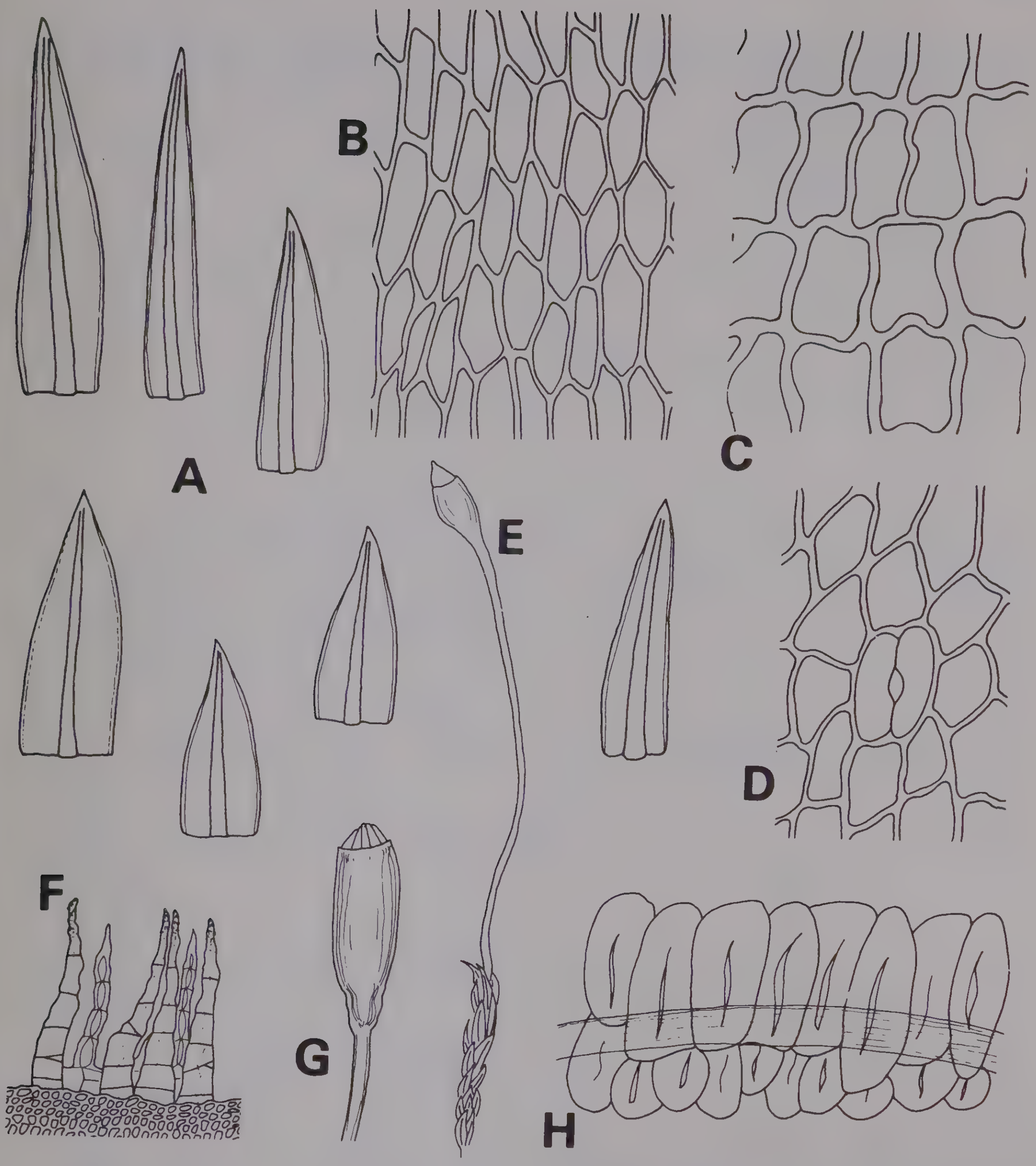


FIG. 19. *Pohlia cardotii.* A. Leaves, ×22. B. Upper leaf cells, ×290. C. Exothecial cells, ×290. D. Stomates, ×290. E. Habit, ×3. F. Peristome, ×80. G. Capsules, ×15. H. Annulus, ×290.

trabeculate; endostome hyaline; basal membrane very low, less than ⅓ the exostome length; segments narrow but somewhat keeled and broadly perforate; cilia rudimentary to lacking. Spores 14–19 μm, finely roughened. Fig. 19.

Uncommon; on soil in alpine or subalpine sites. Apparently endemic to western North America; Alaska, British Columbia, Washington and California. Map 16.

Exsiccati: Allen, Mosses of the Cascade Mts. 56 as *P. porosa* (isotypes, see above for representative herbaria).

A relatively rare alpine species, *P. cardotii* is easily recognized by the erect capsules, very low basal membrane, and especially when sterile, strongly recurved leaf margins and rather thick-walled cells. *Pohlia crudoides* is the only other American species with strongly recurved margins (except that the perichaetial bracts of most are recurved). When sterile, *P. crudoides* is distinguished by the red stems, narrower leaves and longer, thinner-walled cells. Except for one Alaskan specimen of *P. cardotii* their ranges do not overlap.

A type for *P. cardotii* could not be located in Paris. However, the distinctive nature of this species leaves little question of the application of the name. In the future, if an isotype is not found, a neotype should be selected.

16. **Pohlia erecta** Lindb., Bot. Not. 1882: 195. 1882. (Lectotype: H–SOL; Isotypes: H, O, WTU).

Mielichhoferia defecta Sanio, Bot. Centralbl. 13: 248. 1883. (Lectotype: H–SOL).

Webera defecta Sanio, Bot. Centralbl. 13: 248. 1883 (*nom. nud. in synon.—M. defecta*).

Mielichhoferia erecta (Lindb.) Kindb., Forh. Vid. Selsk. Christiana 1888(6): 22. 1888.

Webera erecta (Lindb.) Limpr., Laubm. Deutschl. 2: 239. 1891.

Pohlia defecta (Sanio) Andr. *in* Grout, Moss Fl. N. Am. 2: 189. 71. 1935.

Slender, rather glossy plants. Stems 3–8 mm, generally simple when sterile or bearing perichaetia, with 1–2 innovations when bearing perigonia. Leaves erect-spreading to erect, more or less crowded, lanceolate; 0.7–1.2 mm long, serrate to serrulate near the apex; upper cells rhomboidal, 35–60 μm long, 6–9 μm wide, thin-walled. Dioicous; perichaetial bracts slightly differentiated, to 2.2 mm long; perigonial bracts shortly acuminate, erect. Capsules erect or nearly so, symmetric, slenderly pyriform, 2.0–3.0 mm long; exothecial cells shortly rectangular, 25–60 μm long, with sinuose walls; stomates superficial; annuli of 1(2) cell row(s), separating irregularly; exostome teeth yellow to light brown, narrowly triangular, somewhat irregular, obtuse, papillose (but not coarsely so) near the apices, bordered, ± trabeculate; endostome hyaline; basal membrane very low, less than ⅓ the exostome length; segments rudimentary and irregular or ± elongate and perforate; cilia absent. Spores 15–21 μm, finely roughened. Fig. 20.

Very rare, on soil in the alpine zone. Western North America (Yukon Territory, British Columbia and Washington) and Fennoscandia. Map 17.

The erect capsules resemble those of *P. cardotii*, but the endostome of *P. erecta* is even more reduced. Sanio (1883) described this species as a *Mielichhoferia*. Although *P. erecta* seems at home in *Pohlia*, the distinctions between plants of the so-called Mielichhoferioideae (*Mielichhoferia, Synthetodontium, Haplodontium*) and *Pohlia* are sometimes ill-defined.

Pohlia erecta differs from *P. cardotii* in having soft-textured leaves with plane margins, thinner-walled cells and narrower costae.

When sterile, *P. erecta* resembles a small version of *P. drummondii*, especially in having reddish stems. Further similarities between *P. erecta* and *P. drummondii* include the aspect and branching of male plants (Fig. 20) and strongly sinuose exothecial cells. These combined probably indicate close phylogenetic affinity.

17. **Pohlia beringiensis** Shaw, sp. nov.

Plantae erectae, graciles, plerumque steriles. Caulis simplex, 4–15 mm altus. Folia pallida, erecta, imbricata, lanceolata, ad apicem serrulata, cellulis linearibus. Gemmae frequenter adsunt, oblongae, cerasinae.

Slender, pale-whitish plants diffusely scattered in small populations. Stems 4–15 mm, simple. Leaves erect, imbricate (moist or dry), 0.9–1.3 mm long, 0.3–0.6 mm wide, narrowly lanceolate, gradually acute, slightly decurrent; margins plane, serrulate near the apex, entire below; costa ending 3–5 cells below the apex; upper cells linear-rhomboidal, ± vermicular, thin-walled, 60–90(–100) μm long, 6–10 μm wide, somewhat longer and narrower along the margin. Gemmae single in 1–4 upper leaf axils, oblong-bulbiform, about 500–650(–1000) μm long, deep cherry-red when moist, red or black when dried, with 3–6 large, broadly

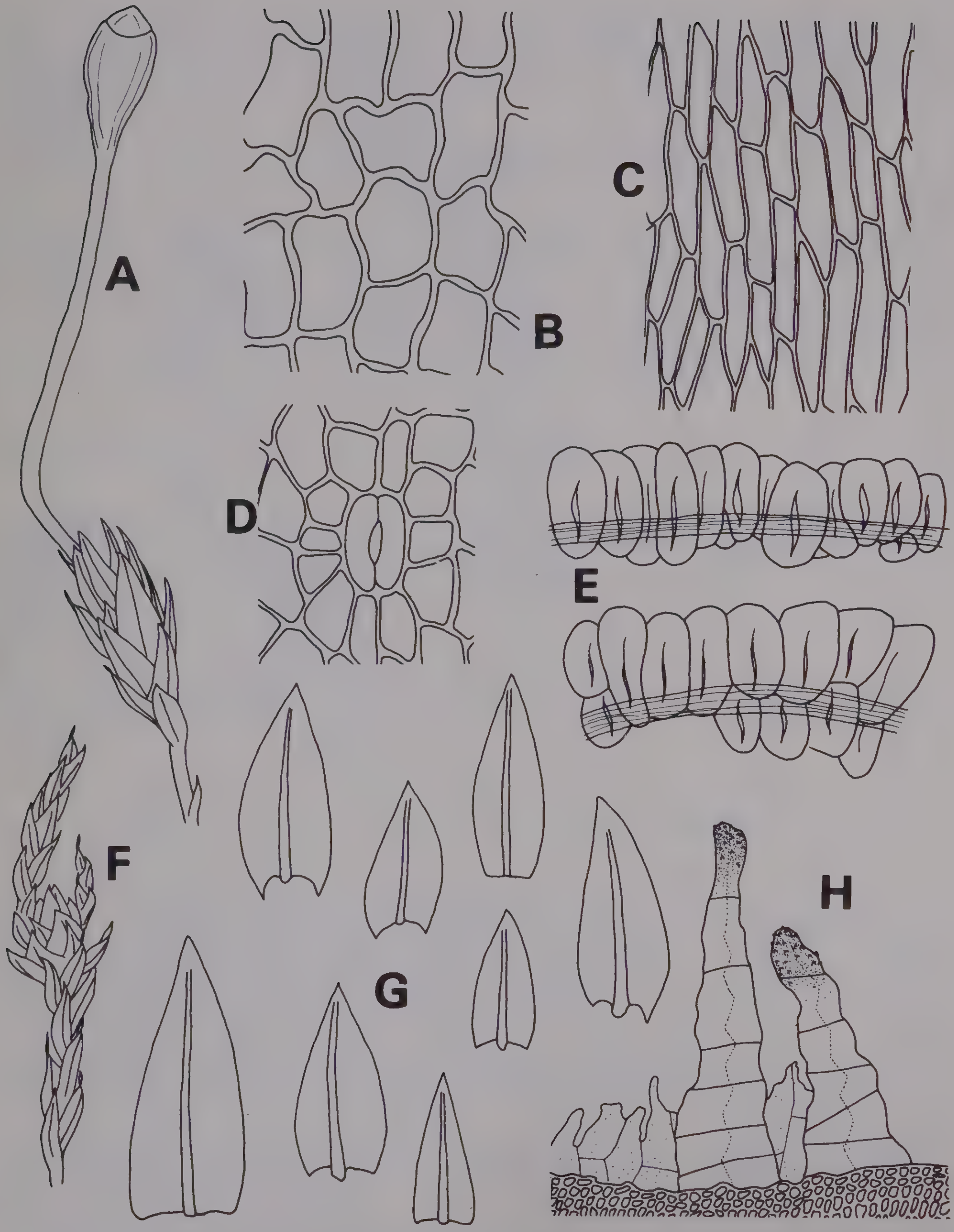


FIG. 20. *Pohlia erecta.* A. Habit, female plant, ×5. B. Exothecial cells, ×290. C. Upper leaf cells, ×290. D. Stomate, ×290. E. Annuli, ×290. F. Habit, male plant showing subfloral innovations, ×5. G. Leaves, ×22. H. Peristome, ×250.

laminate leaf primordia at the apex and frequently lower, the primordia green. Inflorescences and sporophytes unknown. Fig. 21.

TYPE: Alaska, Paxson area, 11.7 km W of Paxson on Hwy. 8., 22 July 1979, *Shaw 3794* (Holotype: MICH). Paratypes: Alaska, Honolulu area, 57.5 km S on Hwy. 3 from junction with Hwy. 8 at Cantwell, 24 July 1979, *Shaw 3889* (ALTA). Yukon Territory, Ogilvie Mts., Tombstone Mt. area, 71.3 km N of Hwy. 3 on the Dempster Hwy., 16 July 1979, *Shaw 3466* (MICH).

On organic-poor soil in mountainous areas, especially in roadside ditches. Central Asia (Altai Mts.) and northwestern North America (Alaska and Yukon Territory). Map 18.

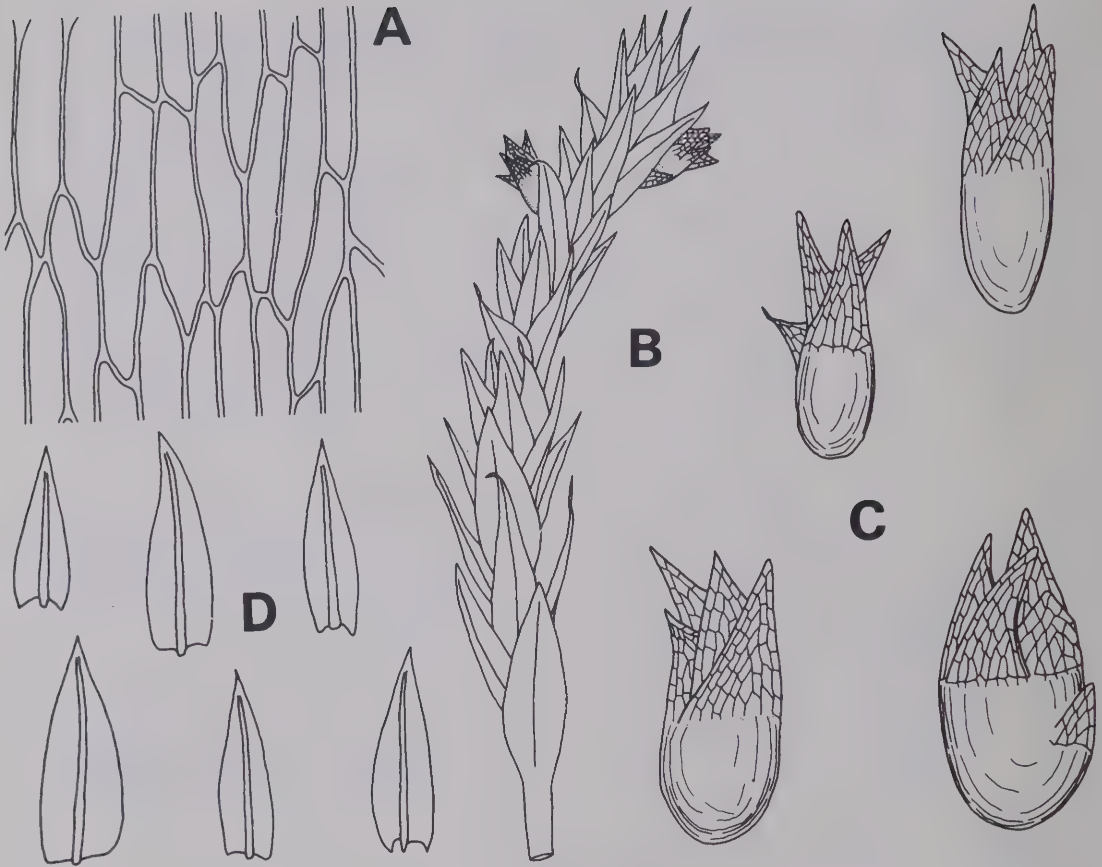


FIG. 21. *Pohlia beringiensis*. A. Upper leaf cells, ×290. B. Habit, ×10. C. Gemmae, ×100. D. Leaves, ×22.

Pohlia beringiensis was mentioned previously (Shaw 1981, p. 33) as a variant possibly related to *P. drummondii*. Continued study has convinced me that it should be segregated as a new species. Compared to *P. drummondii*, plants of *P. beringiensis* are very small, with leaves whitish, erect and slenderly lanceolate. The gemmae are of a similar form to those of *P. drummondii*, but are even more deeply cherry red (at least when fresh). Red gemmae on plants with such pale, whitish leaves gives *P. beringiensis* an aspect different from any expression of *P. drummondii*.

The micro-habitat in which *P. beringiensis* occurs also differs from that of *P. drummondii*. In western North America, *P. drummondii* grows on relatively organic-rich soil banks or frequently in alpine tundra (Shaw 1982), whereas *P. beringiensis* prefers sandy or muddy, organic-poor sites such as roadside drainage ditches. Even allowing for some variation in the microhabitats occupied by *P. drummondii*, there does seem to be ecological differences between the two.

Especially since sporophytes of *P. beringiensis* are not known, differences between it and *P. drummondii* are mainly with respect to aspect, color, size and habitat of plants. The gemmae, in terms of size and development, are similar to those of *P. drummondii*, differing only in color. Varietal status for *P. beringiensis* (under *P. drummondii*) could be defended, and there is no correct answer to the problem of appropriate rank. Other pairs of *Pohlia* species are distinguished by such ill-defined features as habit and color. For example, few collectors confuse *P. melanodon* and *P. wahlenbergii*, although they differ only in size and sheen. The distribution of *P. beringiensis*, seemingly disjunct from central Asia (Altai Mts.) to Alaska and the Yukon Territory, falls more or less within the circumboreal range of *P. drummondii*. In northwestern North America, *P. drummondii* is far more common than *P. beringiensis*. In addition to my own collections of *P. beringiensis* (seven) it has otherwise been collected only twice: Alaska, Liberator Lake, Steere *610723–39* (NY), and U.S.S.R. (or China), Altai Mts., *Barzduna*, 1966 (NICH).

POHLIA ANNOTINA AND RELATED SPECIES

Species of this group, characterized by axillary gemmae, were revised by Shaw (1981a). Brief descriptions, and illustrations of gemmae are provided here but the reader is referred to Shaw (1981a & b) for a more detailed treatment.

All nine species are virtually uniform sporophytically, characterized especially by rectangular, sinuose exothecial cells and well-developed peristomes with endostome segments hyaline, broadly keeled and perforate.

18. **Pohlia drummondii** (C. Müll.) Andr. *in* Grout, Moss Fl. N. Am. 2. 196. 1935.

Medium-sized, glossy plants with red stems (when fresh). Gemmae arising singly in 1–3(–5) upper leaf axils (sometimes lacking in alpine plants), oblong-bulbiform, 350–600 μm long, green when young, red when older, with 3–6 lanceolate-laminate leaf primordia scattered at the apex and below, the primordia generally green. Fig. 22A.

Roadbanks, streambanks and gullies in montane areas, frequent on non calcareous tundra soil. Circumboreal, in North America south to California, Colorado and New England. Map 19.

19. **Pohlia filum** (Schimp.) Mårt., Svensk Vet.–Ak. Arh. Natur. 14: 149. 1956.

Slender, rather glossy plants frequently black below when dry. Leaves erect, imbricate to remote. Gemmae arising singly in 1–3(–5) upper leaf axils, egg-shaped, 300–600 μm long, green when young, orange to orange-brown when older, frequently becoming black when dry, with 3–6 rather stiff, triangular-lanceolate leaf primordia at the apex and sometimes lower, the primordia green to pale. Fig. 22B.

Common on glacial outwash in northwestern North America, rarely along roadsides, restricted to nearly organic-free soils. Circumboreal; in North America south to Oregon, Alberta, Quebec and Prince Edward Island. Map 20.

Pohlia filum is distinguished from *P. drummondii* by its slender habit, erect leaves, and egg-shaped gemmae with stiffly appearing primordia often restricted to the gemmae apex.

20. **Pohlia andalusica** (Höhn.) Broth. *in* Engler and Prantl, Nat. Pfl. 1(3): 551. 1903.

Slender, glossy plants with erect, ± imbricate leaves. Gemmae in clusters of 3–8 in 1–4 upper leaf axils, obconic to oblong, 250–500 μm long, green when young, brown to red-brown when older, with 3–6 lanceolate-laminate leaf primordia more or less restricted to the apex, the primordia green. Fig. 22C.

On soil in disturbed sites; rare in western North America, from Alaska and the Yukon south to Washington and Colorado; more frequent in northern New York, New England and the Maritime provinces. Map 21.

Pohlia andalusica is distinguished from related species by its slender, glossy appearance and gemmae with laminate primordia arising in clusters in a few upper leaf axils.

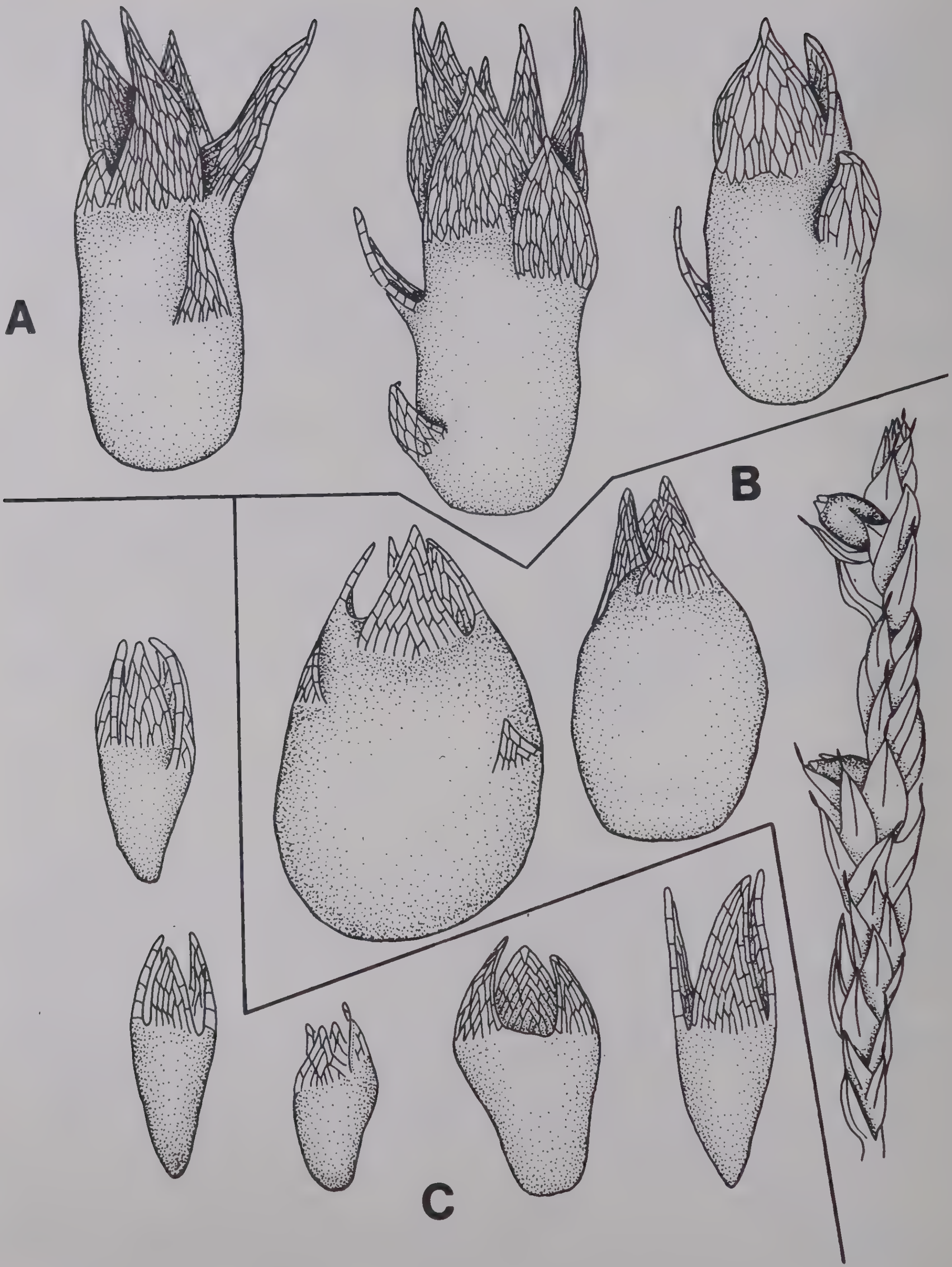


FIG. 22. Gemmae, ×150. A. *Pohlia drummondii*. B. *Pohlia filum*. C. *Pohlia andalusica*.

21. **Pohlia tundrae** Shaw, The Bryologist 84: 65. 1981.

Medium-sized, glossy plants commonly forming compact turfs on tundra soil, more lax and elongate in protected sites. Gemmae in clusters of 3-many in the upper leaf axils, cylindrical to linear-oblong, 275–500 μm long, hyaline, green or red-brown, with 3–6 flexuose, lanceolate-laminate leaf primordia at the apex and frequently lower on the body, the primordia green. Fig. 23A.

Common on alpine and subalpine soil, less frequent along roadbanks and in other disturbed sites below treeline. Endemic to western North America; Wash-

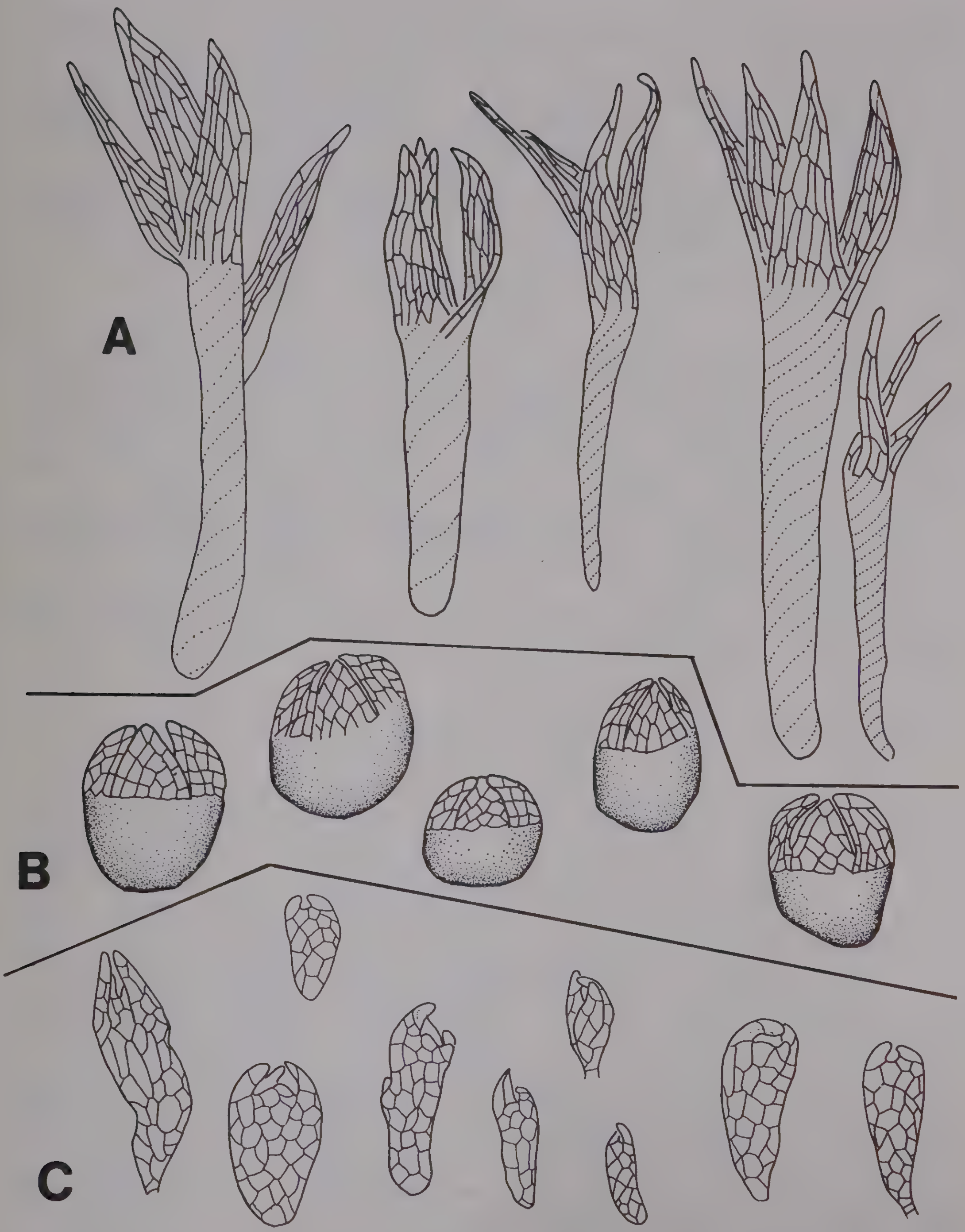


FIG. 23. Gemmae, ×150. A. *Pohlia tundrae*. B. *Pohlia bulbifera*. C. *Pohlia andrewsii*.

ington and Montana south to California and Arizona; northern British Columbia and southern Alaska. Map 21.

The narrowly cylindrical gemmae distinguish *P. tundrae* from other species with laminate leaf primordia. It differs from *P. annotina* in having glossy leaves in addition to the gemmae characters given in the key.

22. **Pohlia bulbifera** (Warnst.) Warnst., Krypt. Fl. Brandenburg 2: 429. 1904.

Slender, glossy plants forming compact turfs. Leaves wide-spreading. Gemmae in clusters of 3–8 in upper leaf axils, spherical to obovate, 200–400 μm in the longest dimension, green to yellow, yellow-orange, or orange-red, with 4–5 broadly triangular-laminate leaf primordia in a tight spiral (almost whorled) at the apex, the primordia green, incurved over the apex and forming a dome. Fig. 23B.

On soil in disturbed places, often where the ground is compacted and hard. Circumboreal; rare in western North America (Alaska, Yukon Territory, Alberta and Colorado), more common in northern New York, New England, and the Maritimes, west to Michigan and Wisconsin. Map 23.

Pohlia bulbifera is known at once by glossy leaves and more or less spheroidal gemmae with the laminate leaf primordia forming a dome over the apex.

23. **Pohlia andrewsii** Shaw, The Bryologist 84: 70. 1981.

Medium size to robust shiny plants forming small populations in rock crevices. Gemmae in clusters of 4-many in the upper leaf axils, oblong to linear-oblong or spheroidal, 50–170 µm long, pale green when young, red to orange-red when older, strongly translucent, with 1–4(–6) short, incurved, peglike leaf primordia at the apex or rarely lower, the primordia of some gemmae becoming laminate with age. Fig. 23C.

Soil in rock crevices in tundra habitats, less commonly along roadbanks. Arctic and subarctic North America, Greenland, Spitzbergen, Norway, Sweden and Czechoslovakia. Map 22.

Pohlia andrewsii may be recognized by glossy leaves and orange to red, translucent gemmae with the primordia, whether peglike or laminate, incurved over the apex.

24. **Pohlia proligera** (Lindb. *ex* Breidl.) Lindb. *ex* Arn., Bot. Not. 1894: 54. 1894.

Medium-sized to robust, glossy plants forming small to extensive populations. Gemmae in dense clusters in upper leaf axils, linear-vermicular to narrowly oblong, 65–110 µm long, green when young, yellow to golden, orange, pink or sometimes red when older, strongly translucent, with 1–2 peglike apical leaf primordia, the primordia (when single) often bent at an angle to the propagulum body. Fig. 24A.

On soil, especially along the sides of roads, paths and streams; sometimes on disturbed tundra soil in the far North but rarely reaching the alpine zone in more southerly mountains; rarely on rotting wood. Circumboreal; our most common propaguliferous species across northern North America, south to California, Colorado, Wisconsin, Michigan and southern New England. Map 25.

Pohlia proligera is well characterized by glossy leaves and linear-vermicular gemmae forming a felty mass in upper leaf axils. The gemmae are uniform in shape and have only one or two apical primordia.

The type specimens of *P. proligera* are located in GJO–Breidler rather than GZU as previously stated (Shaw 1981b, p. 21).

25. **Pohlia annotina** (Hedw.) Lindb., Musci Scand. 17. 1879.

Dull, slender plants often forming ± extensive turfs. Gemmae in clusters of 5-many in the upper leaf axils, extremely variable in shape, oblong, obconic or ± elongate and linear, although almost always tapered to the base, rarely oblong-bulbiform when old, 150–300 µm long, occasionally longer, hyaline, yellow, green, orange or red when young, generally orange-red when large and bulbiform, strongly translucent, with (2–)3–5 peglike, erect, apical leaf primordia, the primordia occasionally becoming 2–4 cells broad at the base on old gemmae. Fig. 24B.

Common in disturbed habitats; sandy soil in gardens, on roadbanks and in gullies, rarely found in undisturbed sites. Possibly circumtemperate; specimens

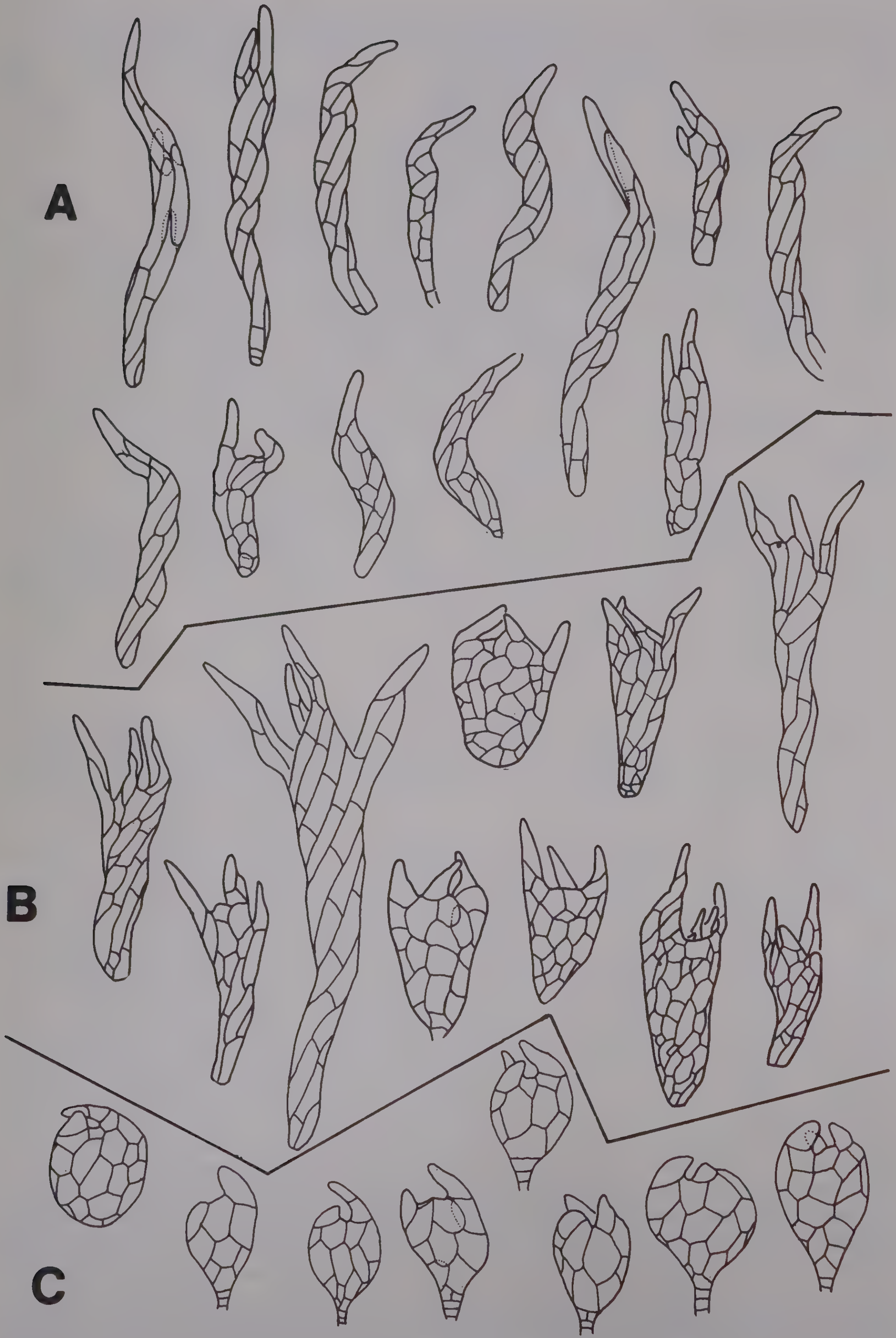


FIG. 24. Gemmae, ×150. A. *Pohlia proligera*. B. *Pohlia annotina*. C. *Pohlia camptotrachela*.

confirmed from northern and central Europe and North America. Bicentric in North America and having a suboceanic distribution: Newfoundland to Georgia and Arkansas, Wisconsin, Missouri and Iowa; Alaska, British Columbia, Montana, Washington, Oregon and California. Map 26.

Characterized by dull leaves and oblong to linear-obconic gemmae with peglike leaf primordia, *P. annotina* can be confused only with *P. camptotrachela*. From *P. proligera* it is distinguished by dull leaves and gemmae having three to as many as five primordia.

26. **Pohlia camptotrachela** (Ren. & Card.) Broth. *in* Engler & Prantl, Nat. Pfl. 1(3): 552. 1903.

Slender, dull plants forming small isolated populations. Gemmae in clusters of 5-many in upper leaf axils, uniform in shape, spheroidal or slightly longer than wide, 70–120(–150) µm in the longest dimension, yellow or occasionally brown, strongly translucent, with 1–4 short, peglike leaf primordia at the apex, the primordia incurved over the apex or less commonly erect. Fig. 24C.

Not uncommon on soil of roadbanks, pathbanks and stream margins in montane areas along the Sierra Nevada–Cascade systems; rather poor alpine soil in the central Rockies. Western North America (British Columbia south to California, Nevada and Colorado); the British Isles, central and northern Europe. Map 27.

Unlike *P. annotina*, the gemmae of *P. camptotrachela* are uniform in shape and size: roughly spheroidal and less than 150 µm in diameter. Among the North American propaguliferous species, only *P. annotina* and *P. camptotrachela* have notably dull leaves. Virtually identical male plants of the two species give further indication of a close relationship.

27. **Pohlia pacifica** Shaw, sp. nov.

Plantae erectae, graciles, valde nigrescentes. Caulis simplex, e basi innovans et ramulosus, erectus, 1.0–8.0 mm altus. Folia inferiora lanceolata, comalia elongato-lanceolata, ad apicem valde serrata, cellulis linearibus, angustis. Peristomia duplices, exostomii dentibus 16, luteo-bruneis. Annulus latus, duplex vel triplex.

Slender, pale green, shiny plants usually in small populations. Stems 2–8 mm, simple when sterile or bearing gametangia. Leaves erect-spreading to spreading when moist, scarcely altered on drying, 1.1–1.8(–2) mm long, 0.5–0.8 mm wide, lanceolate, acute to shortly acuminate, not or slightly keeled, not to slightly decurrent; margins plane, coarsely serrate near the apex, entire to subentire below; costa ending 3–5 cells below the apex; upper cells linear-rhomboidal, vermicular, thin-walled, (100–)115–135(–150) µm long, 6–9 µm wide, somewhat longer and narrower along the margin (to ca. 180–200 µm). Dioicous; perigonia bulbiform; outer bracts ± longly acuminate, spreading to erect-spreading from an erect base, serrate near the apex; perichaetia rather conspicuous, outer bracts to 3.2 mm long, narrowly and longly lanceolate. Sporophytes frequent in spring; setae 5–10 mm long; capsules inclined 120°–180° from vertical, 1.5–2.5 mm long, orange to tan, pyriform, the neck shorter and narrower than the urn; exothecial cells shortly rectangular, 25–55 µm long, 12–25 µm wide, with evenly thickened, strongly sinuose walls; stomata superficial, 35–55 µm long; annuli of 2(3) rows of cells, separating irregularly; opercula convex-conic, obtuse or rarely acute; exostome teeth yellow-brown, narrowly acute, bordered, trabeculate, coarsely papillose near the apex dorsally, more finely roughened below; endostome hyaline; segments keeled and broadly perforate; basal membrane about ½ the height of the exostome teeth; cilia short to long, usually nodulose. Spores 14–20 µm, nearly smooth. Fig. 25.

TYPE: U.S.A. California, Del Norte Co.: Del Norte Redwoods State Park, southern boundary, clay roadbank, 15 April 1980, *Shaw 4173* (Holotype: MICH; Isotype: J. Shaw). Paratypes: Oregon, Tillamook Co.: 2.7 mi N of Arcada Beach on Hwy. 101, muddy roadbanks and drainage ditches, 14 April 1980, *Shaw 4110*

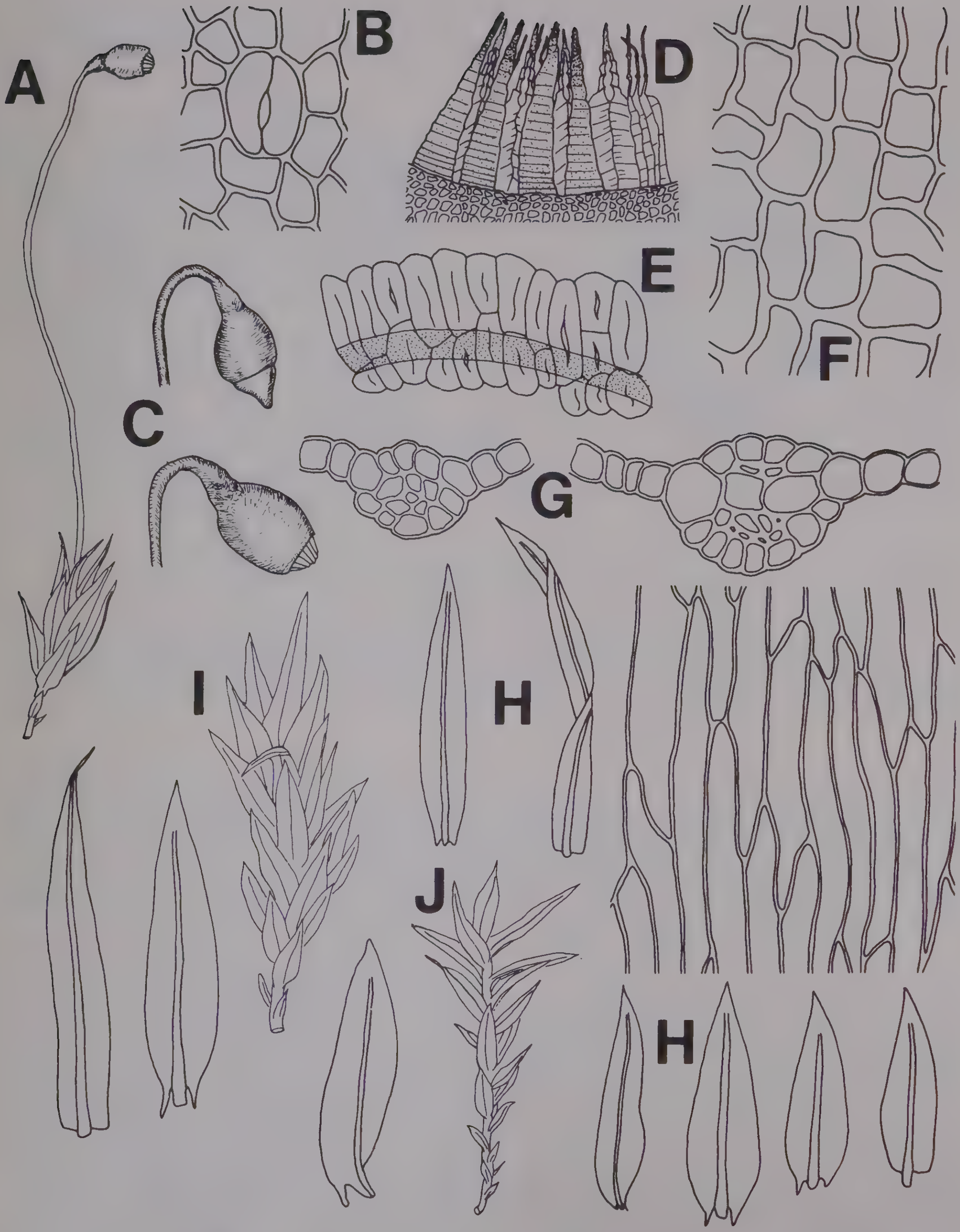


FIG. 25. *Pohlia pacifica.* A. Habit, ×3. B. Stomate, ×230. C. Capsules, ×12. D. Peristome, ×64. E. Annulus, ×232. F. Exothecial cells, ×232. G. Costae, transverse sections near the apex (left) and base (right), ×232. H. Leaves, ×17. I. Habit, female plant, ×3. J. Habit, sterile plant ×3. K. Upper leaf cells, ×232.

(CANM), 4127 (NY). Washington, Clallam Co.: Sol Duc Hot Springs, *Lawton 4298* (WTU).

Acidic, sandy or clay soil, especially in wet, disturbed places at sea level; drainage ditches, stream banks. Endemic to the Pacific Coast of North America; Queen Charotte Islands of British Columbia (*Schofield 14172a*, UBC), Washington, Oregon, California (south to Santa Cruz County). Map 28.

Pohlia pacifica generally grows in the same habitats with *Epipterygium tozeri* (Grev.) Lindb. and *P. longibracteata*. It is frequently mixed with the *Epipterygium*,

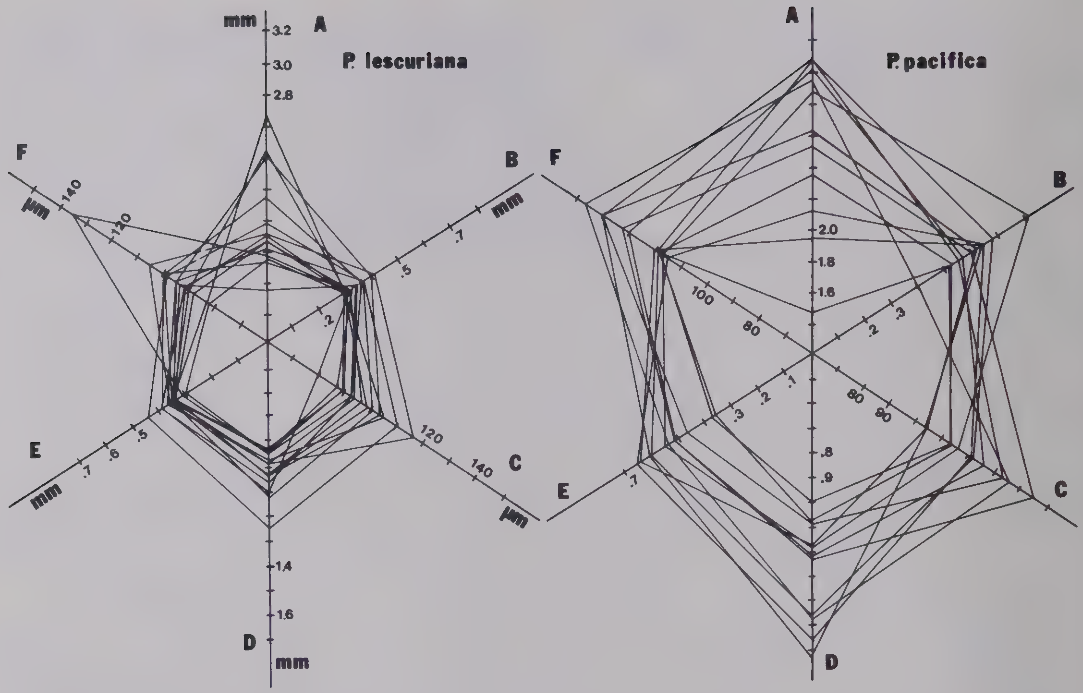


FIG. 26. Polygraph comparing poulations of *Pohlia lescuriana* and *Pohlia pacifica*. A. Perichaetial leaf length. B. Perichaetial leaf width. C. Branch leaf cell length. D. Branch leaf length. E. Branch leaf width. F. Perichaetial leaf cell length. Lines connect values for different measurements from one specimen.

whereas *P. longibracteata* prefers wetter sites (sometimes a few feet away) that are periodically submerged. *Pohlia longibracteata* is much larger (8–15 mm), lacks an annulus and has immersed stomates. *Epipterygium tozeri* is the same size as *P. pacifica* but has dull, bluish leaves, with broad cells (14–25 μm wide), and strongly collenchymatous exothecial cells.

Pohlia pacifica is closely related to *P. lescuriana* but is distinguished by the more robust habit, very glossy leaves and longer cells. Figure 26 compares populations of the two species with respect to six morphological characters; *P. pacifica* is more robust in all respects. Although many populations of *P. lescuriana* have rhizoidal gemmae, I have seen one or two apparently attached to *P. pacifica* only once, as pointed out to me by A. C. Crundwell in a specimen sent for his opinion.

Tan, Shaw and Ireland (1981) reported *P. lescuriana* from western North America, but several of the specimens have proved to be misidentified. I can confirm *P. lescuriana* in the west on the basis of only two collections from Alaska: Curry, *Schofield 1892* (BH); Kenai Peninsula, *Shaw 4016* (MICH).

28. **Pohlia lescuriana** (Sull.) Grout, Moss. Handlens Microsp. 210. 1906.

Bryum pulchellum Hedw., Spec. Musc. 180. 1801.
Hypnum pulchellum (Hedw.) Web. & Mohr, Ind. Musc. Crypt. 3. 1803.
Bryum carneum var. *pulchellum* (Hedw.) Turn., Musc. Hib. 119. 1804.
Mnium pulchellum (Hedw.) P. Beauv., Prodr. 76. 1805.
Bryum tenellum Brid., Bryol. Univ. 1: 653. 1826 (*nom. nud. in synon.—B. pulchellum*).
Webera pulchella (Hedw.) Fuernr., Flora 12(Ergbl. 2): 35. 1829.
W. carnea var. *pulchella* (Hedw.) Hampe, Flora 20: 277. 1837.
Bryum lescurianum Sull., Mem. Am. Ac. Arts. Sci. n. ser. 4: 171. 1849.
Webera lescuriana (Sull.) Jaeg., Ber. S. Gall. Naturw. Ges. 1873–74: 1875.
Pohlia pulchella (Hedw.) Lindb., Musci Scand. 17. 1879.

Webera iwozanica Besch., Ann. Sci. Nat. Bot. ser. 7. 17: 342. 1893.

Mniobryum pulchellum (Hedw.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

Tiny, dull or somewhat glossy plants. Stems 2–8 mm, simple when sterile or bearing gametangia. Leaves erect-spreading on sterile plants, few, erect, and overlapping on fertile plants, 0.8–1.4 mm long, serrulate near the apices; upper cells linear-rhomboidal, 65–110 µm long, 6–9 µm wide, with thin walls. Tubers sometimes present on rhizoids, orange, orange-brown or yellow, 70–120 µm long. Dioicous; perichaetial bracts linear-lanceolate to lanceolate, to 2.5 mm long; perigonial bracts ± longly acuminate, erect to erect-spreading. Capsules inclined 95°–180° from vertical, shortly and broadly pyriform, 1.5–3.0 mm long; exothecial cells short-rectangular, 12–40 µm long, with strongly sinuose walls; stomates superficial or slightly sunken; annuli of 1–3 cell rows, separating irregularly; opercula low to high conic; exostome teeth light yellow-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose, rarely short. Spores 18–26 µm, distinctly roughened. Fig. 27.

Uncommon; on soil, often in weedy places, roadbanks, fields, stream banks, near sea level. Fennoscandia; British Isles; Central Europe; Japan; North America; Maritime provinces and New England south to Virginia and Tennessee, west to Michigan and Iowa; disjunct in Alaska, where it is known from the Kenai Peninsula and near Curry on the southern edge of the Alaska Range. Map 28.

Exsiccati: Austin, Musci Appal. 190 as *B. lescurianum* (CANM, CAS, MICH, UBC); Brotherus, Bryoth. Fenn. 45 as *P. pulchella* (BH); Grout, N. Am. Musci Perf. as *P. lescuriana* (CANM, CAS, COLO, MICH, NY, UBC, UC); Hartman, Bryac. Scand. Exs. 404 as *W. pulchella* (BH); Holzinger, Musci Acro. Bor.–Amer. 220 as *W. lescuriana* (CANM, MICH, UC; =*P. wahlenbergii* in COLO); Husnot, Musci Gall. 572 as *W. pulchella* (BH); Macoun, Canad. Musci 163 as *W. lescuriana* (CANM: =*P. annotina* in UC); Renauld and Cardot, Musci Am. Sept. Exs. 222 as *W. lescuriana* (BH, CANM); Sull., Musci Allegh. 101 as *B. pulchellum* (MICH); Sull. & Lesq., Musci Bor. Am. (ed. 1) 181 as *B. lescurianum* (BH, MICH); (ed. 2) 273 as *B. lescurianum* (BH, CANM, MICH).

One of the tiniest species, *P. lescuriana* looks much like a miniature *P. annotina* without gemmae. It is characterized by the slight stature, well-developed peristome, sinuose exothecial cells, separating annuli and superficial (or slightly sunken) stomates. I find that North American plants sometimes, but not always, have gemmae on their rhizoids. These range from scarce to abundant and are orange to yellow, round to ovoid, 70–120 µm in diameter, and without bulging superficial cells.

The European *P. lutescens* (Limpr.) H. Lindb. is distinguished from *P. lescuriana* by its stellate rhizoidal gemmae (Whitehouse 1973, 1978), although very similar in most other respects. Ecological and phytogeographic information needs to be accumulated with which to evaluate *P. lutescens* as a biological entity.

29. **Pohlia wahlenbergii** (Web. & Mohr) Andr. *in* Grout, Moss Fl. N. Am. 2: 203. 1935.

Hypnum albicans [Wahlenb. *ex*] Web. & Mohr, Ind. Musc. Pl. Crypt. 3. 1803. (*nom. nud.*).

Hypnum wahlenbergii Web. & Mohr, Bot. Taschenb. 280, 475. 1807 (type not seen).

Mnium albicans Wahlenb., Fl. Lapp. 353. 1812 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

Bryum wahlenbergii (Web. & Mohr) Schwaegr., Spec. Musc. Suppl., 1(2): 92. 70. 1916.

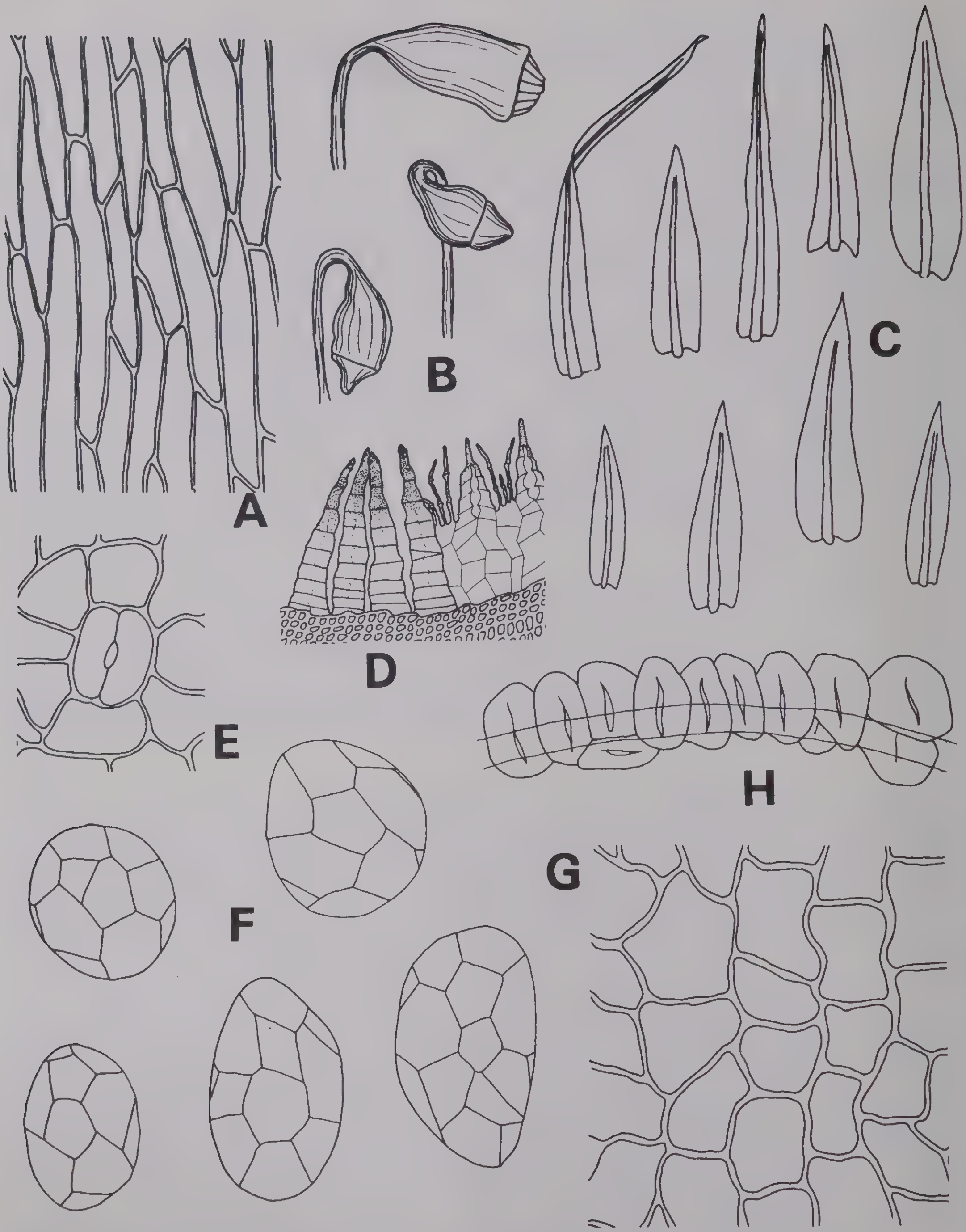


FIG. 27. *Pohlia lescuriana.* A. Upper leaf cells, ×290. B. Capsules, ×15. C. Leaves, ×22. D. Peristome, ×80. E. Stomate, ×290. F. Rhizoidal tubers, ×270. G. Exothecial cells, ×290. H. Annulus, ×290.

B. nitens Sw. *ex* Schwaegr., Spec. Musc. Suppl., 1(2): 92. 1816 (*nom. nud. in synon.—B. wahlenbergii*).

B. glaciale Brid., Bryol. Univ. 1: 852. 1826. (Lectotype: B–Brid.).

Webera wahlenbergii (Web. & Mohr) Fuernr., Flora 12(Ergbl. 2): 35. 1829.

Bryum wahlenbergii var. *glaciale* (Brid.) Hueb., Musc. Germ. 456. 1833.

Webera wahlenbergii var. *glacialis* (Brid.) Hampe, Flora 20: 277. 1837.

Webera albicans Schimp., Coroll. 67. 1856 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

W. albicans var. *glacialis* (Brid.) Schimp., Coroll. 67. 1856.

Lamprophyllum albicans Lindb., Oefv. K. Vet. Ak. Foerh. 23: 75. 1886 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

Pohlia albicans Lindb., Musci Scand. 17. 1879 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

P. albicans var. *glacialis* (Brid.) Broth. & Sael., Act. Soc. F. Fl. Fenn. 6(4): 59. 1890.

Mniobryum albicans Limpr., Laubm. Deutschl. 2: 277. 1892 (*nom. illeg. incl. spec. prior.—H. wahlenbergii*).

Pohlia obtusata Kindb., Rev. Bryol. 32: 37. 1905. (Lectotype: S–Kindb.).

Mniobryum wahlenbergii (Web. & Mohr) Jenn., Man. Moss. W. Penn. 146. 18. 1913.

Mniobryum wahlenbergii var. *glaciale* (Brid.) Wijk & Marg., Taxon 8: 74. 1959.

Very robust to slender, dull, whitish plants forming small populations or covering large areas. Stems 4–15(–50) mm, simple when slender and sterile, forking when robust and fertile, with 1–3 innovations below perichaetia or perigonia; leaves erect-spreading, crowded to remote, 0.9–1.8 mm long, toothed to serrulate in the upper ⅓, acute or sometimes ± rounded at the apex, ± longly decurrent; upper cells broadly oblong-hexagonal, 65–110 μm long, 12–20(–30) μm wide, gradually longer and narrower near the margin, with thin to firm walls. Dioicous; perichaetial bracts scarcely differentiated, to 2.0 mm long; perigonial bracts shortly acuminate, wide-spreading. Capsules inclined 140°–240° from vertical, shortly and broadly pyriform or urceolate, 1.5–2.5 mm long; exothecial cells ± isodiametric, 22–55 μm, with strongly sinuose walls; stomates ± deeply immersed; annuli lacking; opercula low-convex to conic, apiculate; exostome teeth light brown to red-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline to yellow; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 13–18(–24) μm, very finely roughened. Fig. 28.

On calcareous rocks or soil in wet seepy areas, ditches, stream margins, springs, glacial outwash; sea level to the alpine zone. Widespread in North America (across Canada and south to California, Arizona, Arkansas and North Carolina), Europe, and northern Asia; Iceland; Greenland; Mexico (Baja California, Distrito Federal, Michoacán, Oaxaca, Puebla, Sonora); Guatemala (Quezaltenango, San Marcos); Dominican Republic (*Shaw 5656*); Chile; Argentina; Australia (also reported from New Zealand); Japan. Map 29.

Exsiccati: Allen, Moss. Cascade Mts. 53 as *P. albicans* (DUKE, MICH, NFLD); Bauer, Musci Eur. Exs. 915 as *M. albicans* (WTU); Drummond, Musci Amer. 260 as *B. carneum* (CANM, MICH, NY); Grout, N. Am. Musci Perf. 260 as *M. carneum* (UC); Holmen, Bryoph. Dan. Exs. 151 as *W. albicans* (ALTA, NFLD, UC); Holzinger, Musci Acro. Bor.–Am. 168 as *M. albicans* (MICH, UC); 220 as *W. lescuriana* (COLO); 393 as *M. albicans* (MICH, UC); 437 as *M. albicans* (MICH, UC, WTU); Kobsch, Bryoth. Sax. 52 as *M. albicans* (MICH); 244 as *M. albicans* (MICH); 420 as *P. commutata* (MICH); Macoun, Canad. Musci 165 as *W. albicans* (MICH); 208 as *W. carnea* (CANM); Migula, Krypt. Germ., Aust., Helv. Exs. 228 as *M. albicans* (MICH); Rabenhorst, Bryoth. Eur. 1215 as *W. ludwigii* (MICH); Ren. & Card., Musci Am. Sept. Exs. 303 as *W. albicans* (MICH); Savicz-Ljubitzkaja, Hep. Musci URSS Exs. 126 as *M. wahlenbergii* (WTU); 127 as *M. wahlenbergii* v. *glaciale* (WTU); Schofield, Bryoph. Can. 9 as *P. wahlenbergii* (ALTA, CANM, NFLD); Sull. & Lesq. Musci Bor.–Am. (ed. 1) 100 as *B. wahlenbergii* (MICH); 182 as *B. wahlenbergii* (MICH); ed. 2, 274 as *B. wahlenbergii* (MICH); Warnst. Märk. Laubm. 172 as *W. albicans* (CAS).

Distinguished by rather dull, whitish-green leaves, *P. wahlenbergii* is one of the most common Pohlias of the northern United States and Canada. It is most luxuriant in seepy calcareous areas at high altitudes and latitudes, where the stems may attain a height of several centimeters and the leaves are darker green on deep red stems. In ecologically or geographically marginal sites, *P. wahlen-*

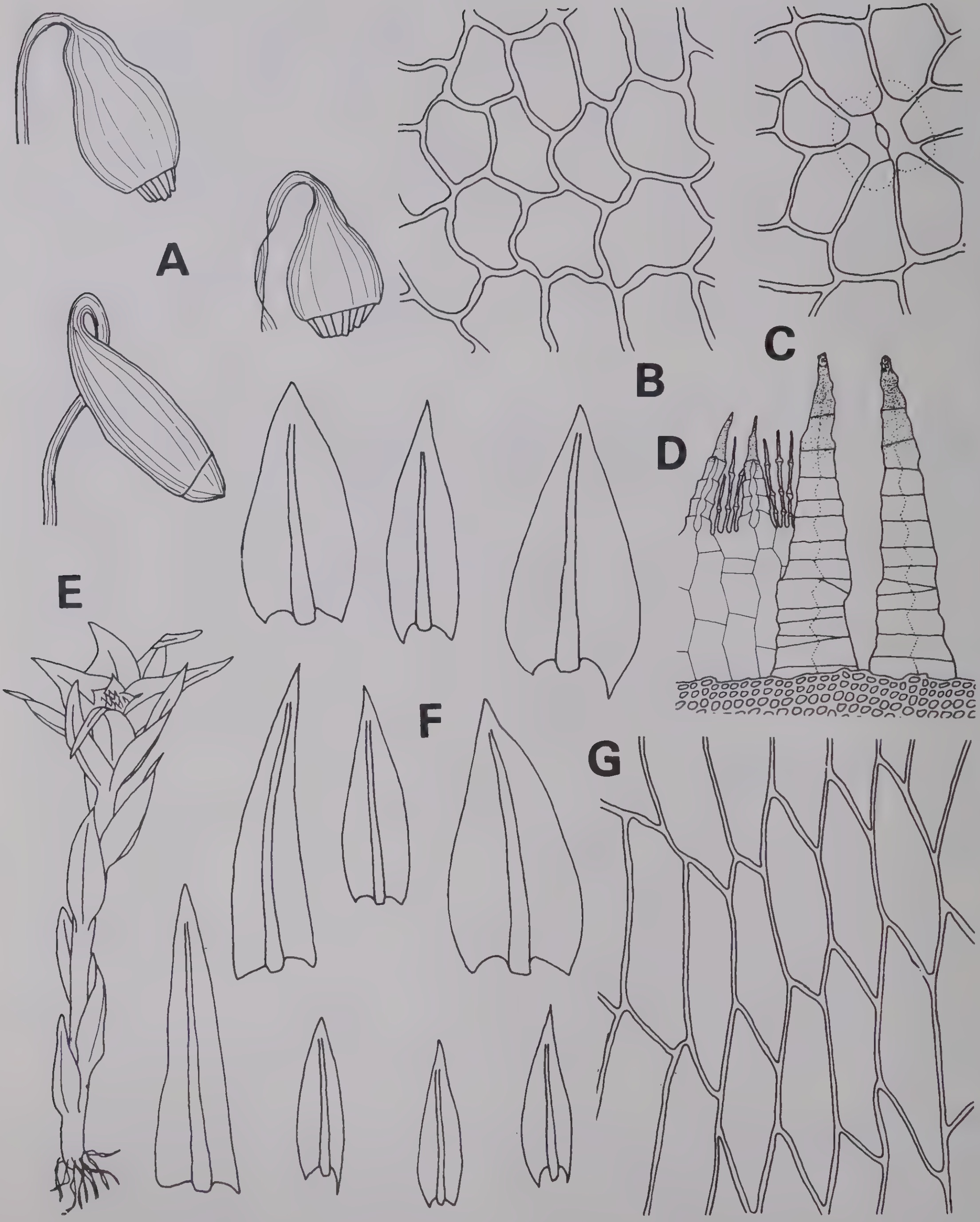


FIG. 28. *Pohlia wahlenbergii*. A. Capsules, ×15. B. Exothecial cells, ×290. C. Stomate, ×290. D. Peristome, ×80. E. Habit, male plant, ×6. F. Leaves, ×22. G. Upper leaf cells, ×290.

bergii may be very slender, with scarcely any superficial resemblance to well-developed forms. The lax cells are helpful in identifying such plants.

Pohlia wahlenbergii, like the following species, produces sporophytes in the spring, and they generally disappear by mid summer. In some areas at least, capsules are abundant in suitably moist sites. All Mexican and Central American collections are sterile.

Small forms may be confused with *P. melanodon,* which is always small but has somewhat glossy, yellow-green leaves that are more acuminate than those of *P. wahlenbergii*. The European *P. wahlenbergii* var. *calcarea* (Warnst.) Warb. is the size of typically well-developed *P. wahlenbergii* but has the gloss and yellowish leaves of *P. melanodon*. The differences between the var. *calcarea* and typical *P. wahlenbergii* are impressive and warrant further study.

Plants collected by A. Radlow in Baja California (50 mi SW of Mexicali, *8504, 8505,* TENN) are less than one centimeter high, green to reddish-brown, somewhat glossy, and have rhomboidal cells (Fig. 29). They are apparently dioicous, but perigonia or sporophytes are lacking. Although in all liklihood distinct, they are included under *P. wahlenbergii* pending further collections. *Pohlia wahlenbergii* has variably shaped cells but they are almost always broader. Among the *Mniobryums, P. longibracteata* and *P. columbica* have cells as narrow as those of the Baja California plants, although in the absence of sporophytes the affinities of the latter is a moot question. The habitat on clay soil along a stream is suggestive of the *Mniobryum* group.

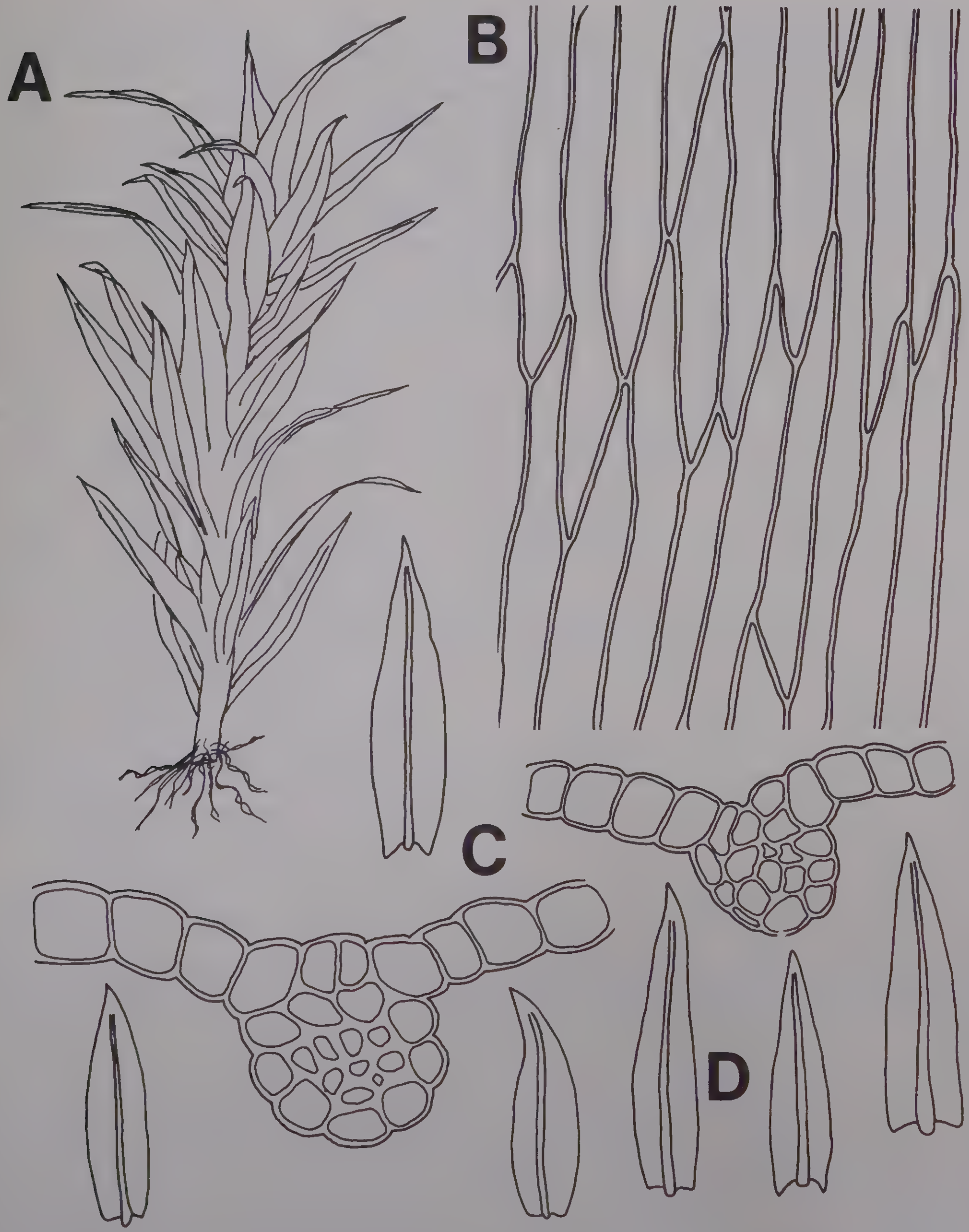


FIG. 29. Plants collected by A. Radlow in Baja California A. Habit, ×30, B. Uppper leaf cells, ×100. C. Costae, transverse sections, ×100. D. Leaves, ×35.

30. **Pohlia melanodon** (Brid.) Shaw, The Bryologist 84: 506. 1982.

Bryum delicatulum Hedw., Spec. Musc. 179. 1801 (type not seen).

Bryum carneum [L. *ex*] With., Syst. Arr. Brit. Pl. ed. 4, 3: 820. 1801 (*nom. illeg. incl. spec. prior.—B. delicatulum*).

Hypnum carneum Web. & Mohr, Ind. Musc. Pl. Crypt. 3. 1803 (*nom. illeg. incl. spec. prior.—B. delicatulum*).

Mnium carneum P. Beauv., Prodr. 74. 1805 (*nom. illeg. incl. spec. prior.—B. delicatulum*).

Bryum melanodon Brid., Bryol. Univ. 1: 845. 1827. (Lectotype: B–Brid.).

Webera carnea Schimp., Coroll. Bryol. Eur. 67. 1855.

Pohlia carnea (Schimp.) Lindb., Musci Scand. 17. 1879.

Webera delicatula (Hedw.) C. Jens., Skand. Bladmfl. 154. 1939.

Pohlia delicatula (Hedw.) Grout, Moss Fl. N. Am. 2: 266. 1940 (*hom. illeg.—P. delicatula* [Mitt.] Broth.).

Slender, glossy, yellow-green plants forming small populations. Stems 2–6 mm, simple when sterile or fertile or rarely with an innovation below perigonia; leaves spreading to erect-spreading, somewhat distant, lanceolate, acute or shortly acuminate, 0.7–1.3 mm long, serrulate near the apex; upper cell laxly and broadly rhomboidal, 60–100 μm long, 10–22 μm wide, somewhat narrower near the margin, with thin walls. Dioicous; perichaetial bracts not strongly differentiated, to 1.9 mm long; perigonial bracts short-acuminate, spreading. Capsules inclined ± 180° from vertical, shortly and broadly pyriform, sometimes urceolate when dry and empty, 1.0–3.0 mm long; exothecial cells isodiametric, ± collenchymatous, 20–45 μm long, with strongly sinuose walls; stomates ± deeply immersed; annuli absent; opercula conic, blunt to acute; exostome teeth dark brown or red-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome yellow to yellow-brown; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 15–22 μm, finely roughened. Fig. 30.

On calcareous clay soil in disturbed, often wet places (ditches, gullies, streambanks, field margins); mostly near sea level. Eastern North America; Ontario and Nova Scotia, New York, New Jersey, Tennessee, Michigan, Ohio and Iowa; Europe; reported from northern Asia; Japan. Sterile specimens from Illinois, Arkansas and Maine probably belong to *P. melanodon*. Map 30.

Exsiccati: Bauer, Musci Eur. Exs. 326 as *M. carneum* (ALTA, BH), 327 as *M. carneum* (ALTA, BH), 1103 as *M. carneum* (ALTA); Erbar, Crittogam Ital. 816 as *W. carnea* (UC); Gyrörffy, Flora Hung. Exs. 929 as *M. carneum* (ALTA, BH, MICH, UC); Harman, Bryac. Scand. Exs. 15 as *W. carnea* (BH); Holmen, Bryoph. Dan. Exs. 152 as *W. delicatula* (ALTA, CAS, UC); Husnot, Musci Gall. 234 as *W. carnea* (BH); Ren. & Card., Musci Eur. Exs. 283 as *W. carnea* (BH); Warnstorf, Märk. Laubm. 173 as *W. carnea* (CAS).

The delicate little plants of *P. melanodon* are best recognized by their glossy yellowish leaves and small capsules with dark-brown exostome teeth, yellow endostomes and deeply sunken stomates. Other than in size and sheen, there is little to distinguish this species from *P. wahlenbergii*, yet the two are rarely confused.

Pohlia melanodon is similar to *P. atropurpurea* and *P. brevinervis*, but the three differ in leaf areolation. In *P. atropurpurea*, the cells of leaves on sterile plants are broad and lax (11–20 μm wide), whereas those of perichaetial bracts are narrow and hexagonal (7–11 μm wide). *Pohlia brevinervis* has narrow, linear cells throughout and *P. melanodon* has lax cells throughout. These differences, though not absolute, help distinguish collections lacking sporophytes (Fig. 32).

Several *Mniobryum* species have exothecial cells just below the rim lax, thin-

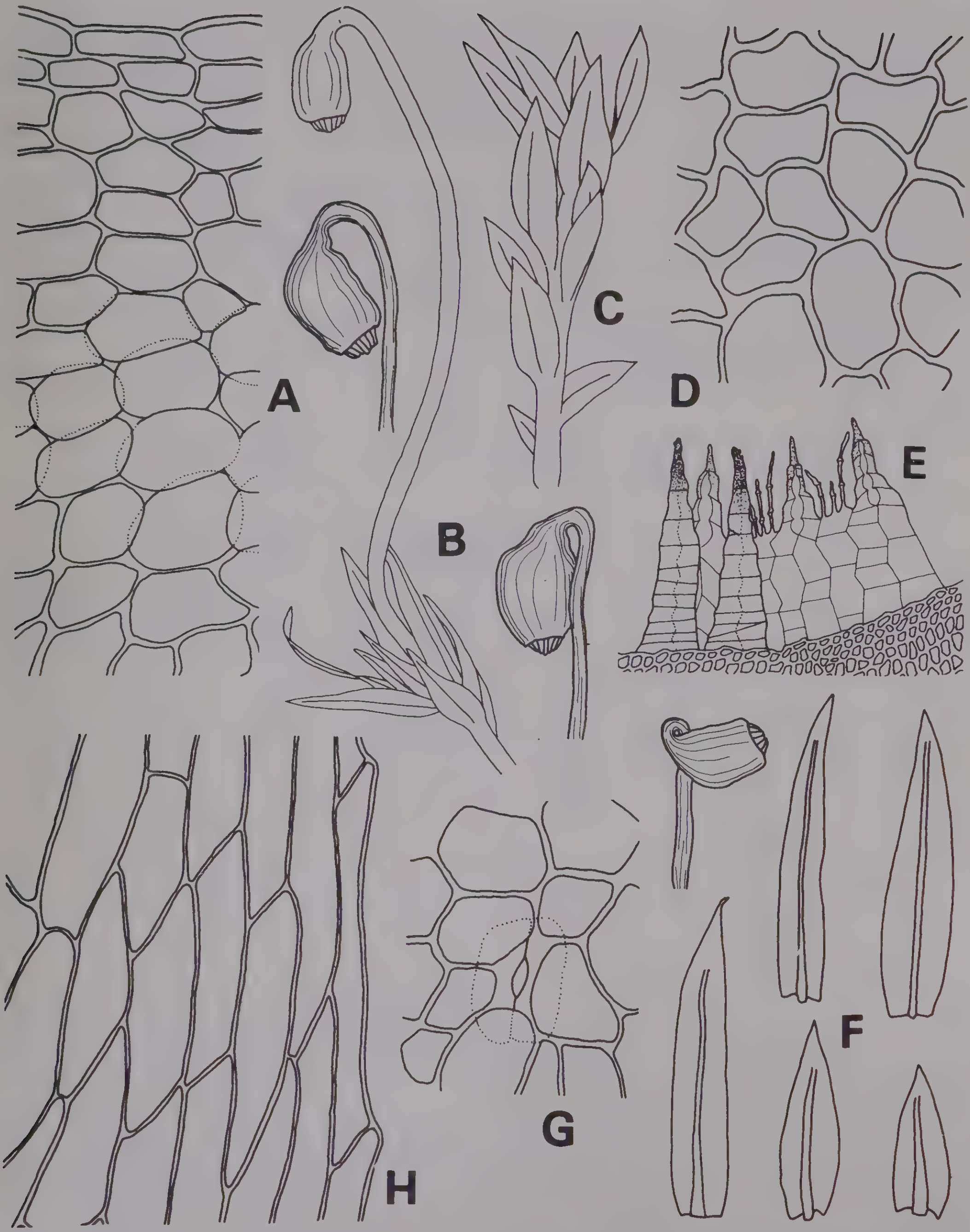


FIG. 30. *Pohlia melanodon.* A. Exothecial cells near the rim, ×290. B. Habit, female plant and capsules, ×8. C. Habit, sterile plant, ×10. D. Exothecial cells, ×290. E. Peristome, ×80. F. Leaves, ×22. G. Stomate, ×290. H. Upper leaf cells showing gradation in shape toward the margin, ×290.

walled and somewhat overlapping (Fig. 30). This is visible under a dissecting microscope as a pale, narrow strip between the urn and rim. It is particularly visible in *P. melanodon* and *P. atropurpurea*, but is also present in such other (non-Mniobryum) species as *P. lescuriana*.

31. **Pohlia atropurpurea** (Wahlenb.) H. Lindb., Acta Soc. F. Fl. Fenn. 16: 14. 1–7. 1899.

Bryum atropurpureum Wahlenb. *ex* Web. & Mohr., Ind. Pl. Crypt. 4. 1803. *nom. nud.*

Bryum pulchellum var. *atropurpureum* Wahlenb., Fl. Lapp. 360. 1812. (Lectotype: S).

B. carneum var. *atropurpureum* (Wahlenb.) Wahlenb., Fl. Lapp. Suppl. 1(2): 91. 1816.

B. atropurpureum (Wahlenb.) Wahlenb. *ex* Fuernr., Flora 12(Ergbl.): 56. 1829.

B. carneum var. *minus* De Not., Syll. 120. 1838 (*nom. illeg. incl. var. prior.—B. carneum* v. *atropurpureum*).

Pohlia borealis Arn. *ex* H. Lindb., Act. Soc. F. Fl. Fenn. 16: 14. 1899 (*nom. nud. in synon.—P. atropurpurea*).

P. arnellii H. Lindb., Act. Soc. F. Fl. Fenn. 16: 14. 1899 (*nom. nud. in synon.— P. atropurpurea*).

P. bardoensis Arn. *ex* H. Lindb., Act. Soc. F. Fl. Fenn. 16: 16:14. 1899 (*nom. nud. in synon.—P. atropurpurea*).

Webera atropurpurea (Wahlenb.) Warnst., Verh. Bot. Ver. Brandenburg 42: 202. 1901.

Mniobryum atropurpureum (Wahlenb.) Hag., Musc. Norv. Bor. 114. 1901.

Webera atropurpurea (Wahlenb.) C. Jens., Skand. Bladmfl. 155. 1939.

Tiny green or reddish plants generally scattered singly with other mosses. Stems 2–6 mm, simple when sterile or fertile. Leaves erect to erect-spreading, distant on sterile stems, overlapping on fertile stems, lanceolate, 0.6–1.3 mm long, serrulate near the apices; upper cells of leaves on sterile plants broadly rhomboidal, 65–110 μm long, 10–15 μm wide, thin-walled, those of the perichaetial bracts narrower (6–11 μm wide). Dioicous; perichaetial bracts ± differentiated, linear-lanceolate, to 3 mm long; perigonial bracts short-acuminate, erect-spreading to spreading. Capsules inclined ± 180° from vertical, shortly pyriform when mature, urceolate when dry and empty, 1.0–2.5 mm long; exothecial cells isodiametric, 15–50 μm long, with strongly sinuose walls; stomates superficial, slightly sunken or ± immersed; annuli lacking; opercula conic, acute; exostome teeth dark brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome yellow to yellow-brown; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 15–21 μm, finely roughened. Fig. 31.

On calcareous, clay soils in wet places (roadbanks, ditches, stream margins), frequently mixed with *P. vexans* and *Bryobrittonia longipes*; low-montane boreal and subarctic habitats, sometimes higher in the mountains. Northern North America; Alaska, Yukon Territory, British Columbia, Washington, Minnesota, Manitoba, Ontario, Iowa, Idaho, and New York; Europe and Asia. Map 30.

Pohlia atropurpurea is characterized by its tiny size, shortly urceolate capsules, almost superficial stomates, dark-brown exostome teeth and yellow endostomes. *Pohlia vexans* is easily separated by its lighter exostome teeth and hyaline endostome.

Although *P. atropurpurea* can be distinguished from *P. melanodon* by several morphological features, the two are obviously closely related. *Pohlia atropurpurea* is a smaller plant and may represent a northern sister species to the more temperate *P. melanodon*. They occupy virtually identical habitats on wet clay soil and when either species grows in the same site with *P. wahlenbergii*, they prefer slightly elevated, presumably drier microhabitats.

32. **Pohlia brevinervis** Lindb. & Arn., Musci Asiae Bor. 51. 1890. (Lectotype: H–SOL).

Webera brevinervis (Lindb. & Arn.) Kindb., Enum. Bryin. Exot. 108. 1891.

Small to very small, whitish, somewhat glossy plants. Stems 2–15 mm, generally simple when sterile or bearing perichaetial, sometimes innovating when bearing perigonia. Leaves erect to erect-spreading, ± crowded and

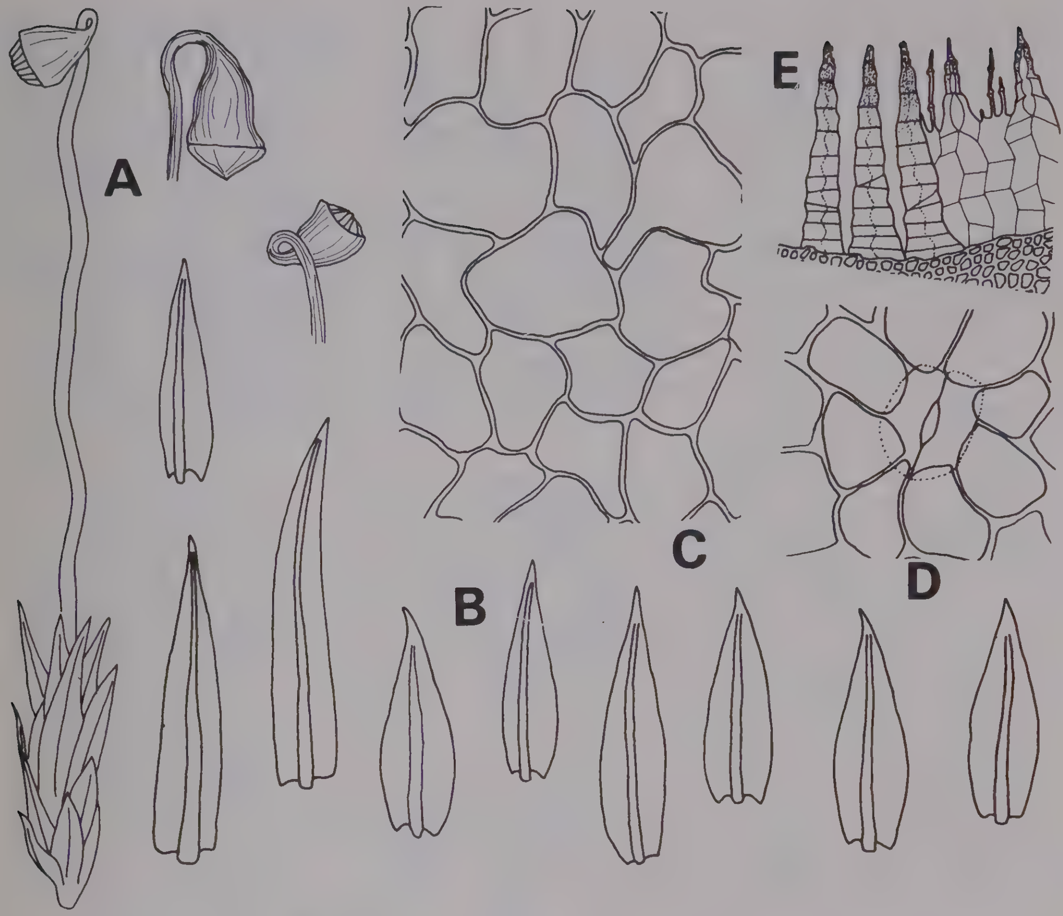


FIG. 31. *Pohlia atropurpurea.* A. Habit, ×12. B. Leaves, ×22. C. Exothecial cells, ×290. D. Stomate, ×290. E. Peristome ×80.

imbricate, lanceolate, 0.7–1.4 mm long, serrulate near the apices; upper cells linear-rhomboidal, 60–110 μm long, 6–9 μm wide, with thin walls. Dioicous; perichaetial bracts slightly differentiated, to 1.9 mm long; perigonial bracts short- to long-acuminate, erect or somewhat spreading. Capsules 150°–180° from vertical, shortly pyriform, 1.0–3.0 mm long; exothecial cells isodiametric, somewhat collenchymatous, 20–40 μm in diameter, with strongly sinuose walls; stomates superficial or somewhat sunken; annuli lacking; opercula conic; exostome teeth dark to light brown or red-brown, acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome light yellow; basal membrane slightly more than ½ the exostome length, segments keeled, broadly perforate; cilia long, nodulose. Spores 16–21 μm, finely roughened. Fig. 33.

On clay soil along streams, outwash and other wet places in subarctic and arctic, montane habitats. Western Siberia and northwestern North America (Alaska, Yukon Territory, and Alberta). Map 31.

This very rare species has been collected fewer than ten times. It is known from six localities in western North America, all close to or within areas thought to be ice-free during the last glacial episode.

On the basis of the few specimens available, *P. brevinervis* is distinguished by relatively elongate stems with erect, whitish leaves, dark exostome teeth, yellow endostomes and slightly sunken stomates. The habit of sterile plants resembles *P. vexans* because of the erect, somewhat shiny leaves, but in sporophytic features *P. brevinervis* resembles *P. atropurpurea.*

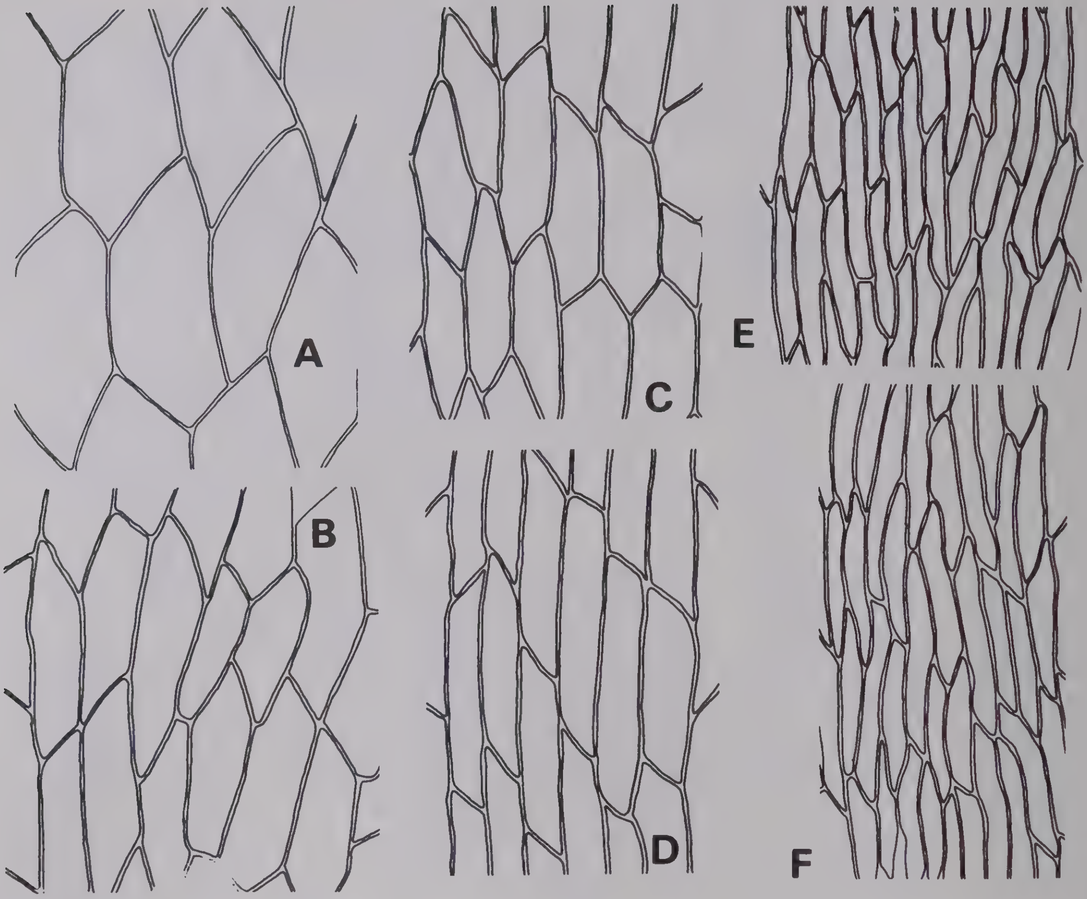


FIG. 32. Upper cells from branch leaves of sterile plants versus perichaetial bracts in "Mniobryum" species, ×260. A–B. *Pohlia melanodon.* A. Branch leaf cells. B. Perichaetial bract. C–D. *Pohlia atropurpurea.* C. Branch leaf. D. Perichaetial bract. E–F. *Pohlia brevinervis.* E. Branch leaf. F. Perichaetial bract.

33. **Pohlia vexans** (Limpr.) H. Lindb., Acta Soc. F. Fl. Fenn. 16: 20. 1899.
Mniobryum vexans Limpr., Laubm. Deutschl. 2: 273. 1892. (Lectotype: BP).
Webera vexans (Limpr.) Par., Ind. Bryol. 1361. 1898.

Slender, glossy plants scattered singly or gregarious, sometimes forming extensive turfs. Stems 5–15 mm, generally simple when fertile or sterile. Leaves erect, imbricate to remote, lanceolate, 0.6–1.3 mm long, serrulate near the apex; upper cells linear-rhomboidal, 70–110 μm long, 6–9 μm wide, with thin walls. Dioicous; perichaetial bracts somewhat differentiated, to 1.8 mm long; perigonial bracts short to long-acuminate, spreading to erect-spreading. Capsules ± 180° from vertical, shortly pyriform, 1.0–3.0 mm long; exothecial cells irregularly isodiametric, 15–45 μm in diameter, with slightly to strongly sinuose, evenly thickened walls; stomates ± deeply immersed, rarely almost superficial; annuli lacking; opercula conic, apiculate; exostome teeth yellow or light brown; acute-triangular, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 17–23 μm, finely roughened. Fig. 34.

Fairly common on calcareous clay soils in wet or moist places (streambanks, roadbanks and other disturbed sites). North-western North America (Alaska, Yukon Territory, Northwest Territories, British Columbia, Alberta, Montana,

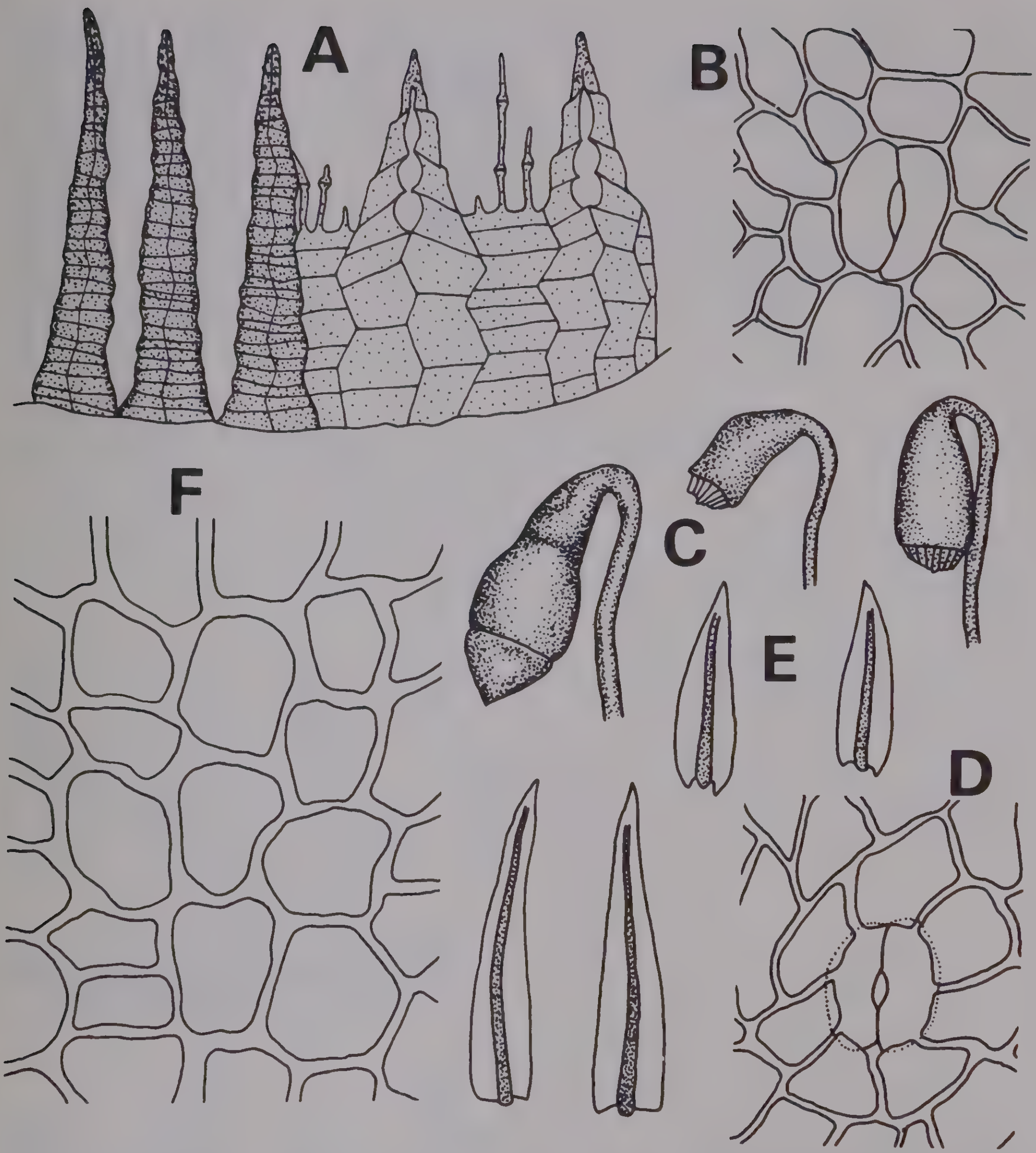


FIG. 33. *Pohlia brevinervis.* (From the Bryologist: in press, 1982) A. Peristome, ×13. B. Stomate, ×490. C. Capsules, ×15. D. Stomate, ×490. E. Leaves, ×33. F. Exothecial cells, ×490.

Manitoba); northern and central Europe; reported from northern Asia by Crundwell and Nyholm (1977). The dot map showing the distribution of this species obviously represents collection localities along the Alaska Hwy. rather than the actual distribution of *P. vexans* populations. Map 32.

Exsicatti: Bauer, Musci Eur. Exs. 328 as *M. vexans* (BH), 1628 as *M. vexans* (WTU); Husnot, Musci Gall. 826 as *W. lutescens* (BH); Macoun, Flora Canadensis 628a as *B. pulchellum* (CANM).

Pohlia vexans is best recognized by erect, glossy leaves on a red stem (at least when moist). It is more common than *P. atropurpurea* and *P. brevinervis*, occurring along many of the sizable streams with clay banks in Alberta, British Columbia and the Yukon. It is restricted to soils of high pH, 6.5 or above.

34. **Pohlia columbica** (Kindb. *in* Macoun & Kindb.) Andr. *in* Grout, Moss. Fl. N. Am. 2: 202. 1935.
Webera columbica Kindb. *in* Macoun & Kindb., Cat. Canad. Pl. 6: 115. 1892.

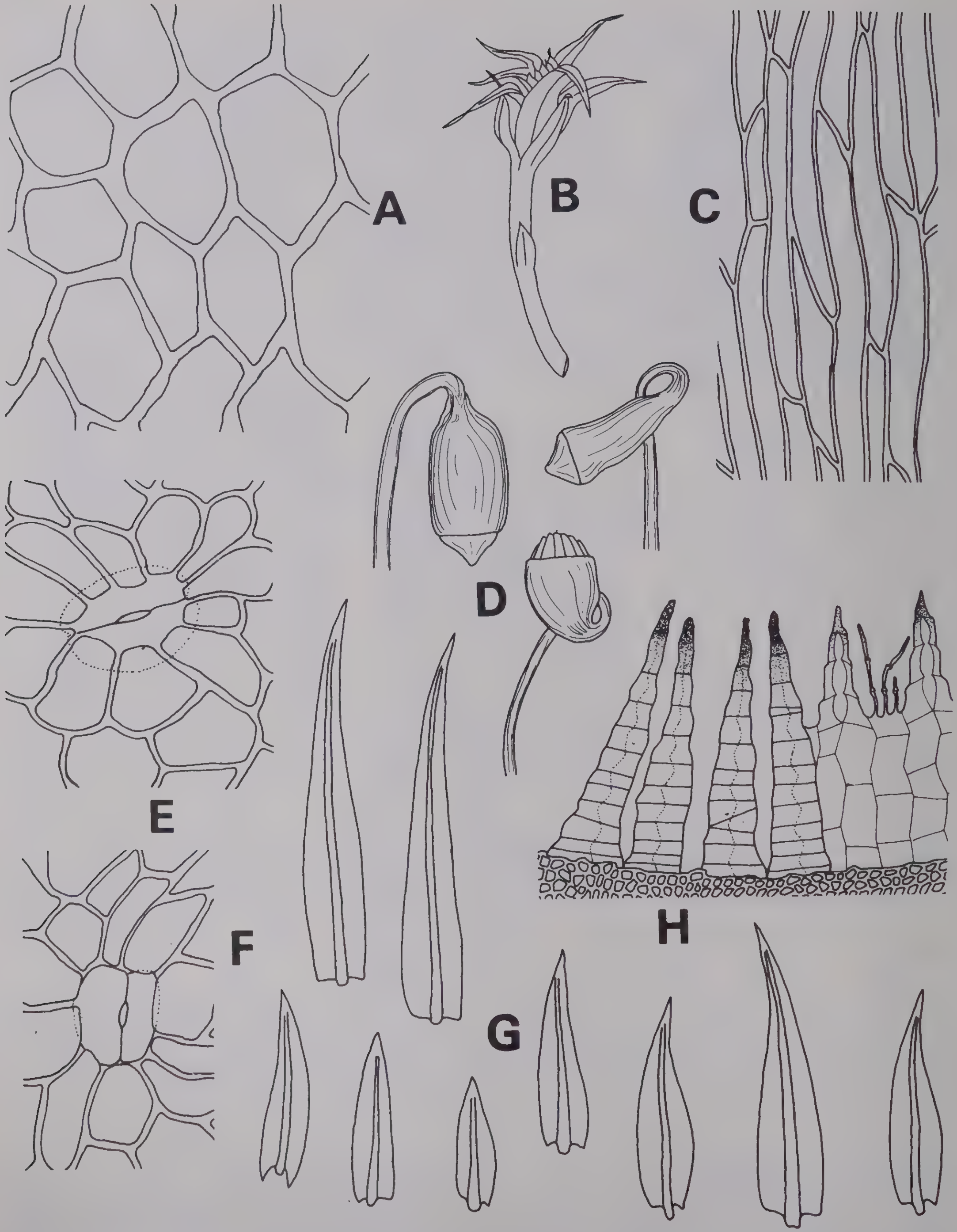


FIG. 34. *Pohlia vexans.* A. Exothecial cells, ×290. B. Habit, male plant, ×7. C. Upper leaf cells, ×290. D. Capsules, ×15. E–F. Stomates, ×290. G. Leaves, ×22. H. Peristome, ×80.

(Lectotype S–Kindb.).

Bryum columbicum (Kindb. *in* Macoun & Kindb.) Kindb., Eur. N. Am. Bryin. 2: 386. 1897.

Pohlia decurrens H. Lindb., Act. Soc. F. Fl. Fenn. 16: 12. 1899. (*nom. illeg. incl. spec. prior.—W. columbica*).

Mniobryum columbicum (Kindb. *in* Macoun & Kindb.) Loeske, Stud. Morph. Syst. Laubm. 124. 1910.

Slender, green or reddish, rather dull plants. Stems 4–8 mm, simple when sterile or fertile. Leaves erect-spreading or spreading, rather distant, narrowly lanceolate to lanceolate, 1.4–2.5 mm long, serrate near the apex or to midleaf; upper cells linear-hexagonal, 85–150 μm long, 6–10 μm wide, with thin walls. Dioicous; perichaetial bracts ± differentiated, linear-lancelate, to 3.0 mm long; perigonial bracts rather long-acuminate, wide-spreading. Capsules inclined 100°–180° from vertical, broadly pyriform or urceolate, 1.5–3.5 mm long; exothecial cells isodiametric, somewhat collenchymatous, 20–40 μm in diameter, with strongly sinuose walls; stomates immersed; annuli lacking; opercula conic, acute; exostome teeth yellow or light brown, acuminate, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline or very pale yellow; basal membrane slightly more than ½ the exostome length; segments keeled, broadly perforate; cilia long, nodulose. Spores 13–18 μm, nearly smooth. Fig. 35.

Very rare; on soil in disturbed places and along streams; mostly near sea level along the Pacific Coast. Apparently endemic to coastal Alaska, British Columbia and Washington. Map 33.

This species is close to *P. longibracteata* but is distinguished by its duller, often reddish leaves, and less conspicuously long perigonial bracts. Whereas *P. longibracteata* is common along the Pacific coast, *P. columbica* is exceedingly rare. I have had no success finding it at the type locality or elsewhere near the coast, although W. B. Schofield has collected it in several places in British Columbia.

The Japanese *P. fauriei* (Card.) Ochi, including *Webera densiretis* Broth., is a rather puzzling, variable intermediate between *P. columbica* and *P. longibracteata*, but according to Ochi (1959) distinct from both. Shiny plants of *P. fauriei* that look like compact expressions of *P. longibracteata* lack the diagnostic very long perigonial bracts. This small complex of the three closely related species is of some phytogeographic interest since they are endemic to the North Pacific region.

35. **Pohlia longibracteata** Broth. *in* Roell, Bot. Centralbl. 44: 419. 1890. (Lectotype: H–SOL).

Webera longibracteata (Broth. *in* Roell) Ren. & Card., Rev. Bryol. 19: 66. 1892.

Bryum longibracteatum (Broth. *in* Roell) Kindb., Eur. N. Am. Bryin. 2: 384. 1897.

Webera lachenaudii Card. & Thér. *in* Bailey, Bryologist 7: 66. 1904. (Isotype: BH, CANM, UC).

Robust, shiny plants forming small populations. Stems 5–25 mm, generally simple when sterile or fertile. Leaves wide-spreading, narrowly and longly lanceolate, distant to crowded, 2–3.5 mm long, rather coarsely serrate near the apices; upper cells linear-hexagonal, 80–160 μm long, with thin walls. Dioicous; perichaetia terminal, or on short, axillary branches; perichaetial bracts ± differentiated, to 4 mm long; perigonia terminal or on short, axillary branches; perigonial bracts extremely long-acuminate, to 6 mm long, wide-spreading. Capsules inclined ± 180° from vertical, broadly pyriform to urceolate, 1.5–3 mm long; exothecial cells isodiametric, 20–40 μm in diameter, with straight to sinuose walls; stomates immersed; annuli lacking; opercula shortly to longly and obliquely rostrate; exostome teeth light-brown to yellow, acuminate, most coarsely papillose near the apices, bordered, trabeculate; endostome hyaline; basal membrane slightly more than ½ the exostome height; segments keeled, broadly perforate; cilia long, nodulose. Spores 14–20 μm, almost smooth. Fig. 36.

Fairly common on calcareous, neutral or mildly acidic soils in wet, often disturbed places at sea level (ditches, gullies, roadbanks, stream margins).

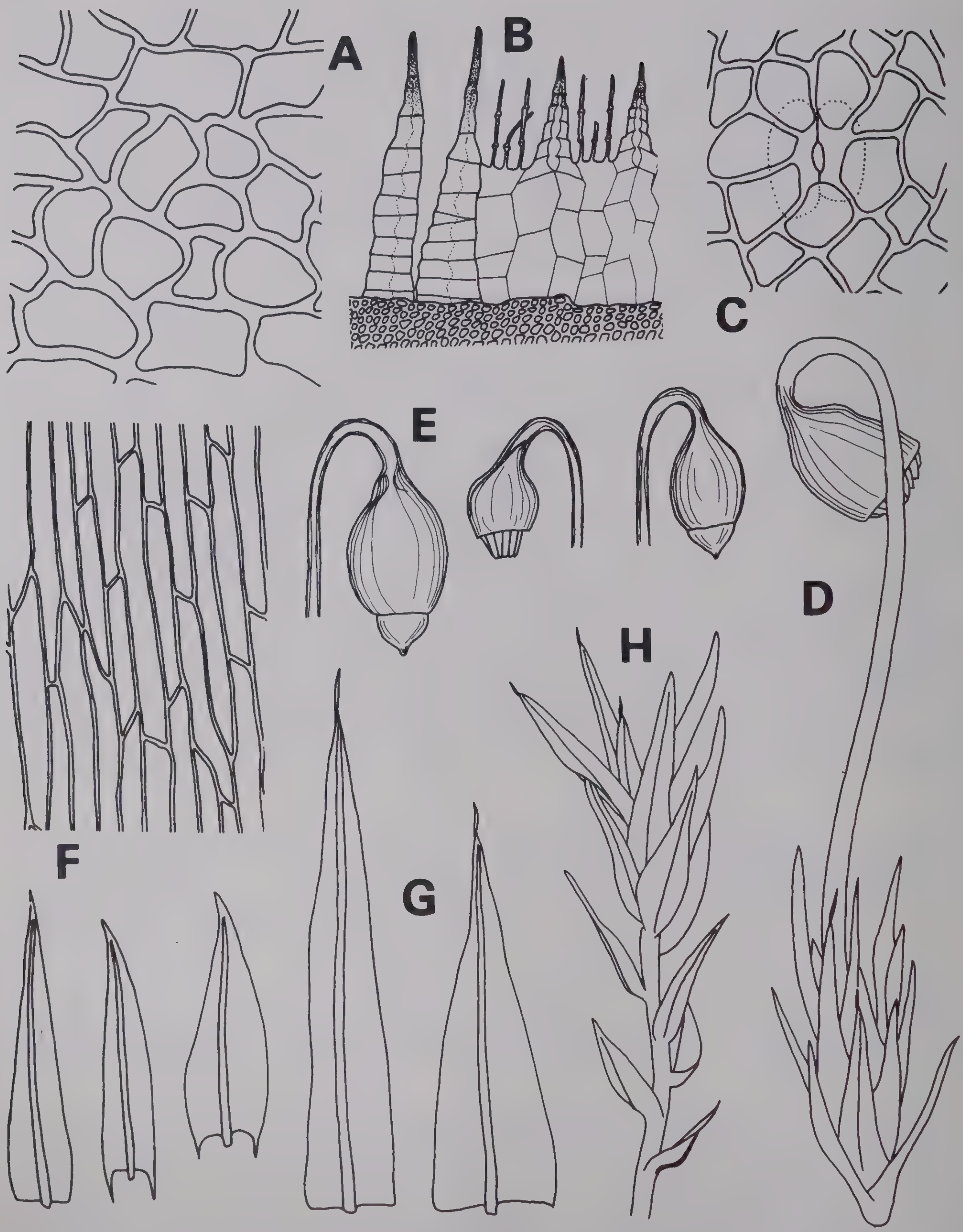


FIG. 35. *Pohlia columbica*. A. Exothecial cells, ×290. B. Peristome, ×80. C. Stomate, ×290. D. Habit, ×9. E. Capsules, ×15. F. Upper leaf cells, ×290. G. Leaves, ×22. H. Habit, sterile plant, ×9.

Endemic to western North America; British Columbia, Washington, Oregon and California (south to Santa Clara Co.). Map 34.

Exsiccati: Grout, N. Am. Musci Perf. 135 as *M. albicans* (MICH); Holzinger, Musci Acro. Bor.–Am. 95 as *W. lachenaudii* (BH, CANM, UC).

Our only common *Pohlia* along the coast of California, Oregon and Washington, *P. longibracteata* is striking because of its large size and very glossy leaves. It is most common along roadsides in wet ditches, but can also be found in undisturbed sites such as muddy streambanks in Redwood forests. The name refers to the perigonial bracts, which are very conspicuous, reaching six millimeters in length.

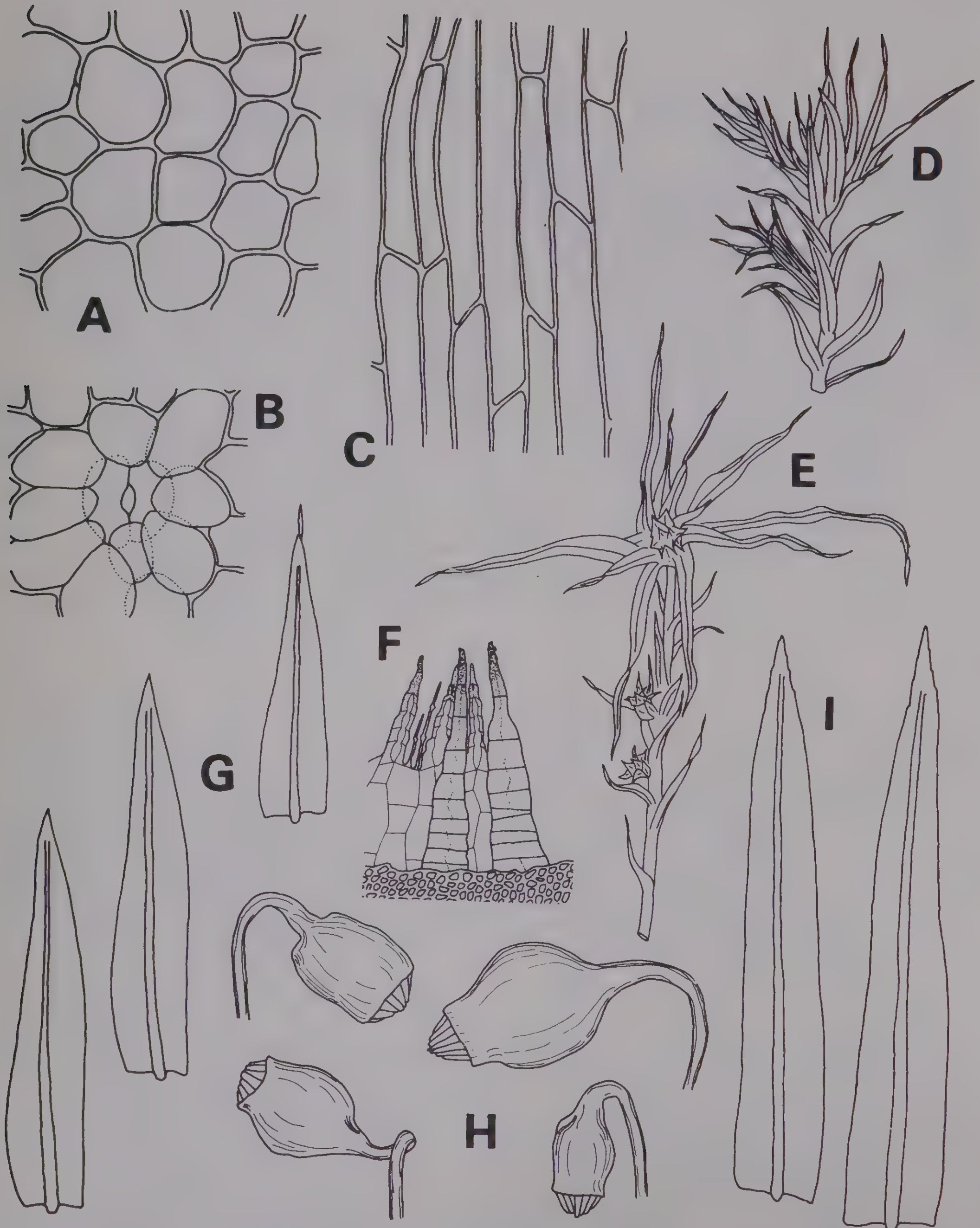


FIG. 36. *Pohlia longibracteata.* A. Exothecial cells, ×290. B. Stomate, ×290. C. Upper leaf cells, ×290. D. Habit, female plant with perichaetia terminal and on short axillary branches, ×4. E. Habit, male plant with terminal and axillary perigonia, ×4. F. Peristome, ×80. G. Leaves, ×22. H. Capsules, ×15. I. Perichaetial bracts, ×22.

It is an interesting feature of *P. longibracteata* that although the inflorescences are generally terminal, it is not uncommon to find them also on short, axillary branches (Fig. 36). Such lateral inflorescences are of the same sex as those that are terminal on the main stem. I have not found any autoicous plants.

36. **Pohlia integra** (Card.) Shaw, comb. nov.

Webera integra Card., Rev. Bryol. 38: 4. 1911. (Isotypes: BH, BM, MO, US).

Mniobryum integrum (Card.) Broth. *in* Engler & Prantl, Nat. Pfl. ed. 2, 10: 362. 1924.

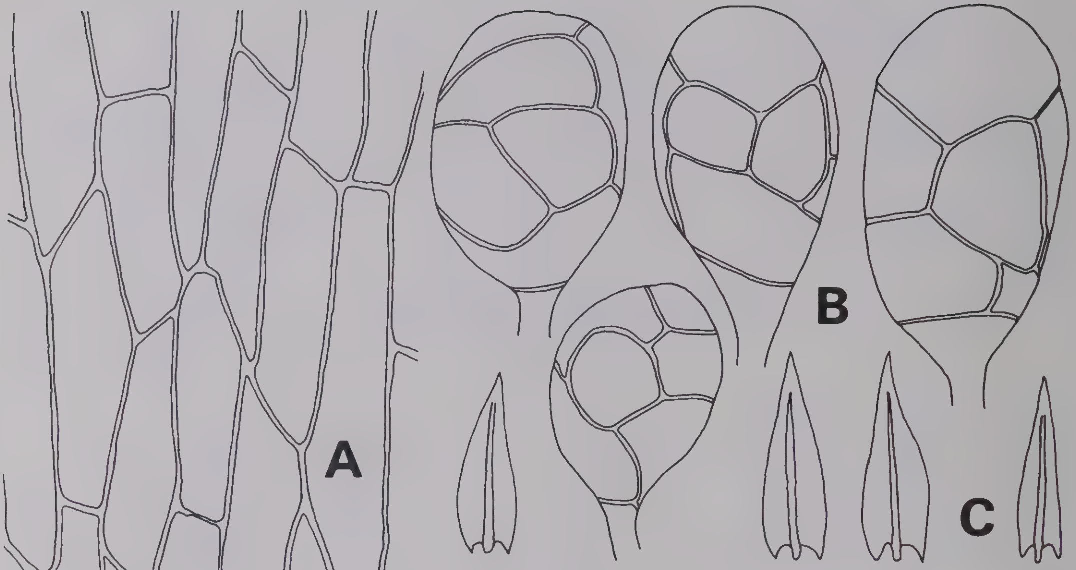


FIG. 37. *Pohlia integra.* A. Upper leaf cells, ×290. B. Rhizoidal tubers, ×200. C. Leaves, ×22.

Very small, pale green to yellow-green, glossy plants. Stem up to 28 mm high, simple. Leaves delicate, flexuose when dry, rather distant, 0.6–1.3 mm long, entire to crenulate near the apices; upper cells laxly elongate-hexagonal, 70–140 μm long, 13–20 μm wide, with thin walls. Gemmae abundant on matted rhizoides at the stem base, also present but infrequent on single rhizoids in the leaf axils, round or more commonly oblong, red-brown, 140–240 μm in the longest dimension; consisting of about 10–14 ± isodiametric cells, each about 90 μm in diameter, the superficial cells not bulging. Inflorescences and sporophytes unknown. Fig. 37.

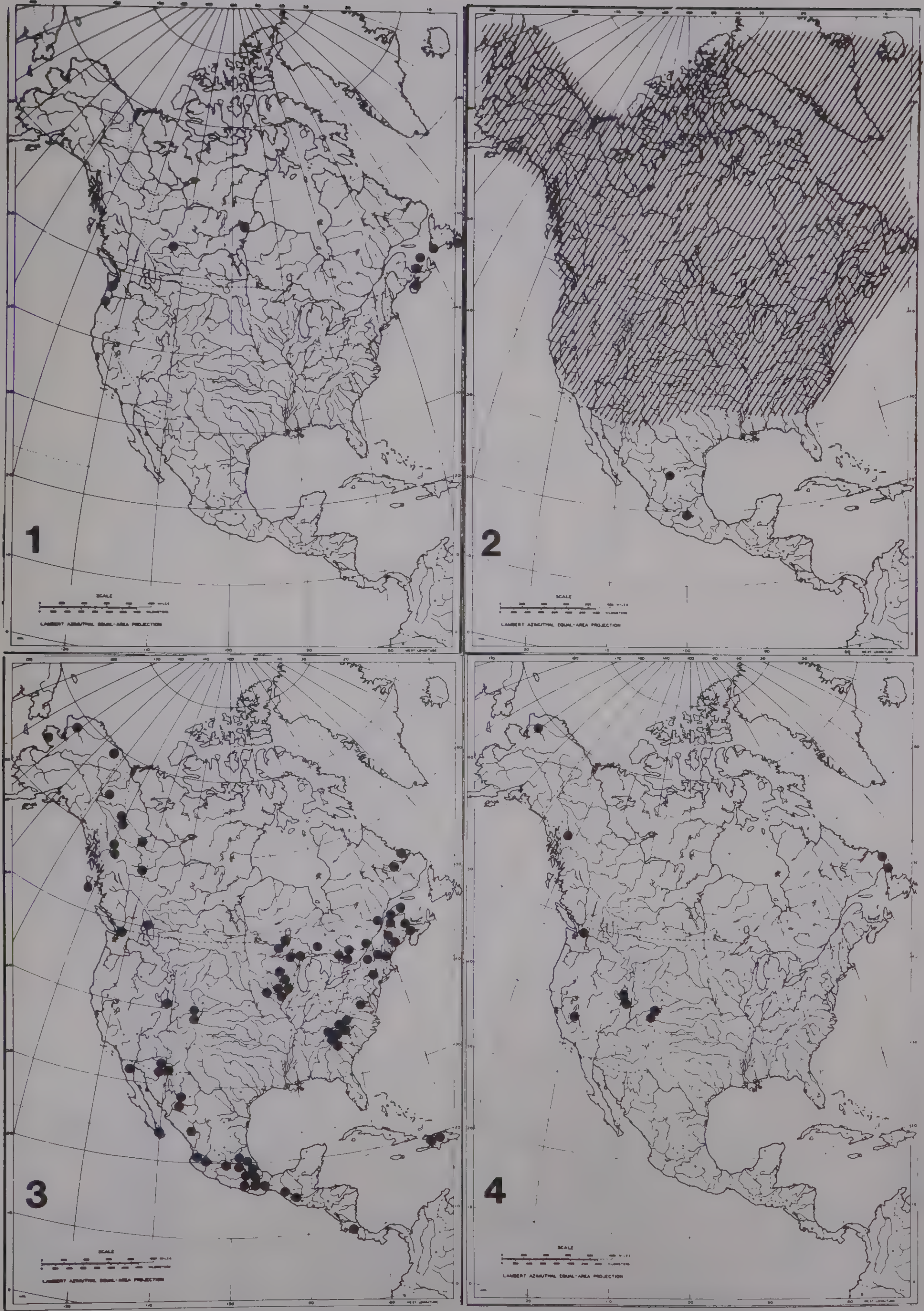
On calcareous clay in rock crevices; endemic to central Mexico (Ixtaccíhuatl). Map 35.

Although *P. integra* is known only from the type locality, the original specimen must have been copious for isotypes are present in a number of herbaria. I have not seen a specimen from the Cardot herbarium in Paris, but since the type material seems to be uniform it would be surprising if such a specimen differs significantly from others.

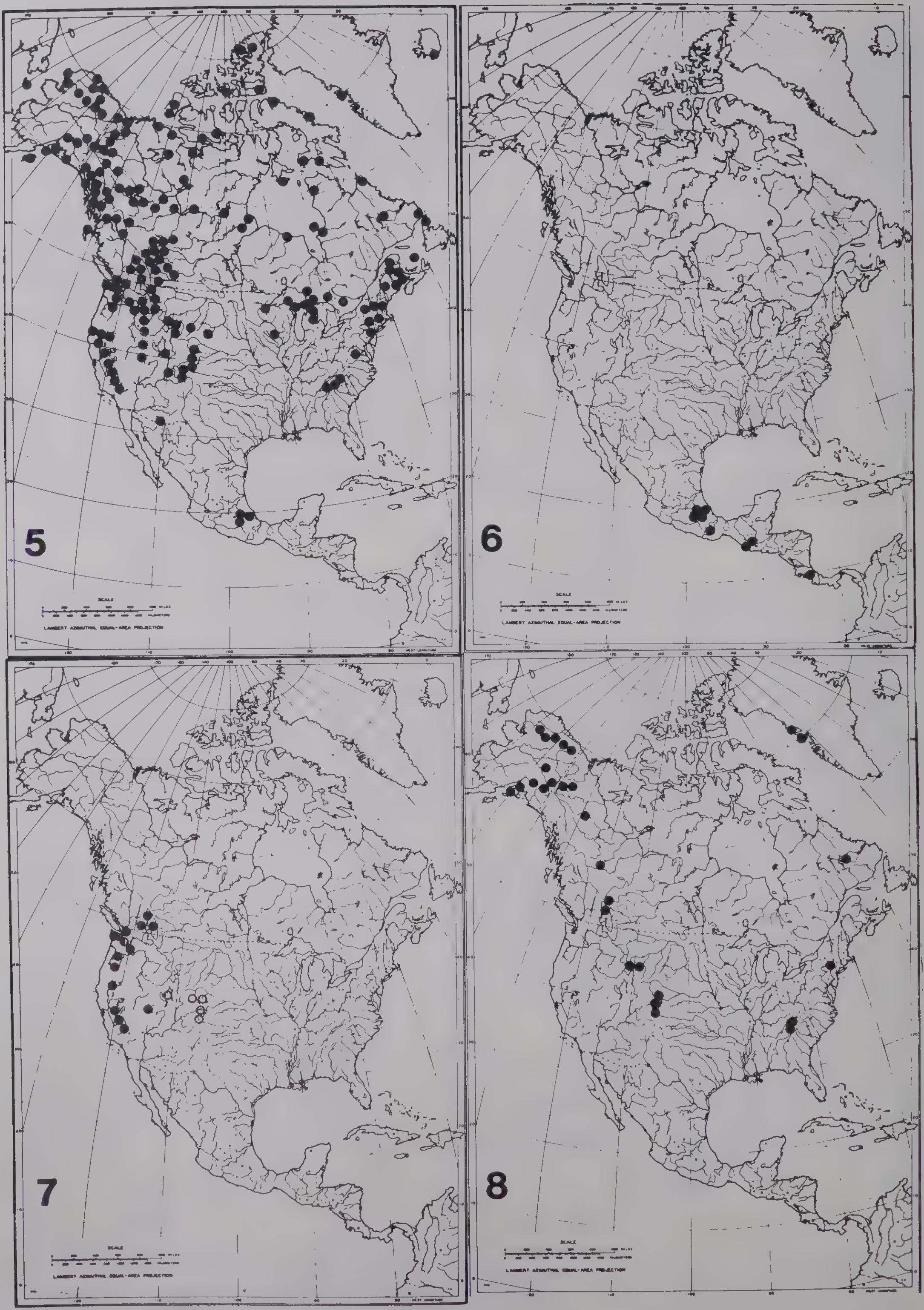
Although sterile, a relationship to the previous "Mniobryum" species is indicated by the lax leaf cells. *Pohlia integra* is distinguished most readily by abundant, deep red, rhizoidal tubers. Compared to *P. wahlenbergii*, which also occurs in central Mexico, *P. integra* has more yellowish, glossy leaves.

DOUBTFUL TAXA

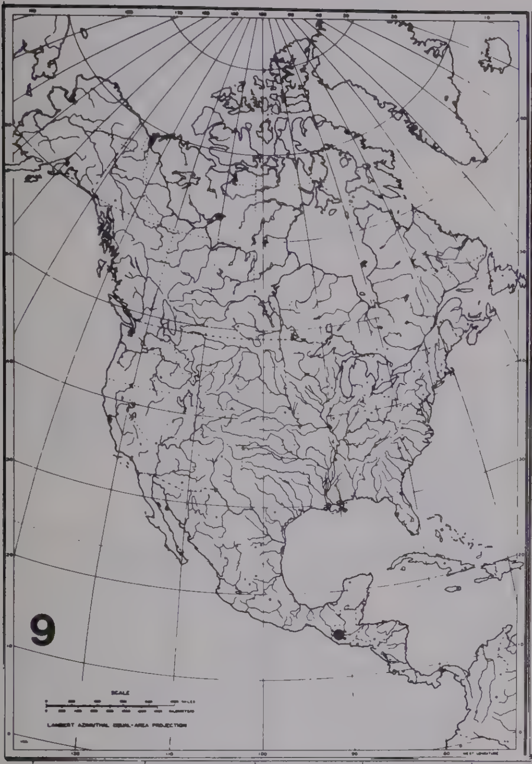
Type specimens for a relatively extensive list of species described by Hoppe and Hornschuch and other early authors were not available for study. Such early names could prove important if types are found in the future. *Webera microapiculata* C. Müll. & Kindb. *in* Macoun, Cat. Canad. Pl. 6: 115. 1892: A type for this species is in the Kindberg herbarium. It is dioicous, lacks sporophytes, and has erect, somewhat glossy leaves. Although it does not agree with any of the species included here, it hardly seems distinctive enough to recognize at present. Only additional collections will help distinguish it as a good species rather than an aberrant form of something else, perhaps *P. cruda.*

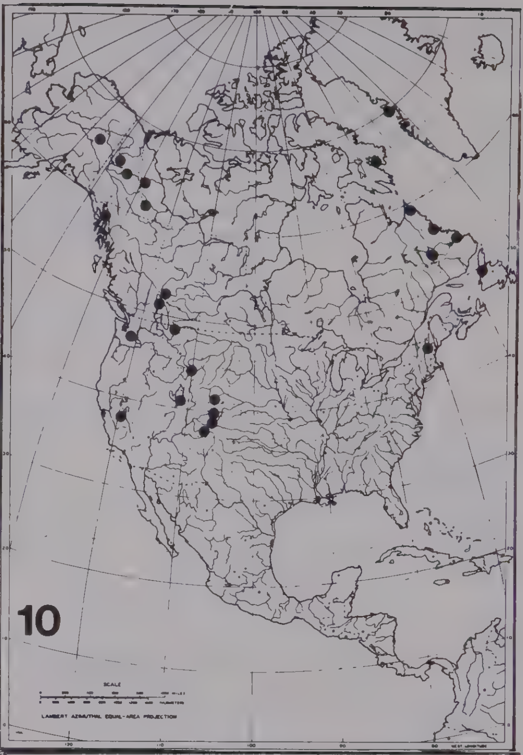


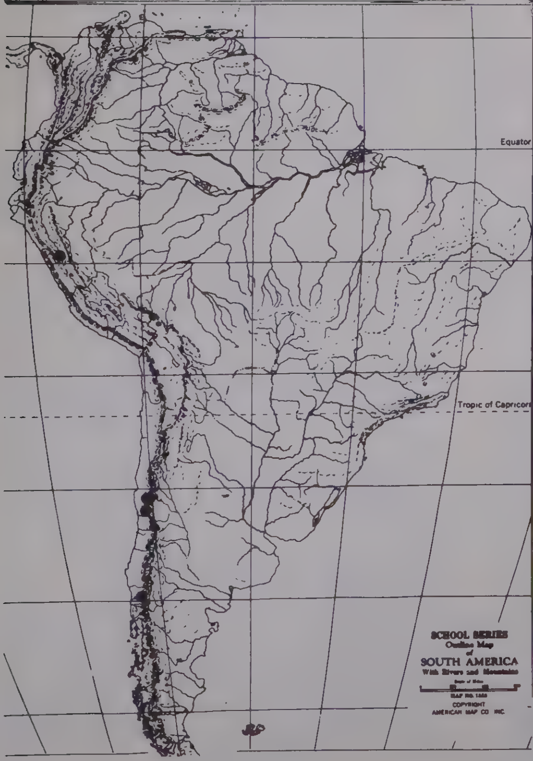
MAPS 1–4. 1. *Pohlia sphagnicola*. 2. *Pohlia nutans*. 3. *Pohlia elongata* var. *elongata*. 4. *Pohlia elongata* var. *greenii*.

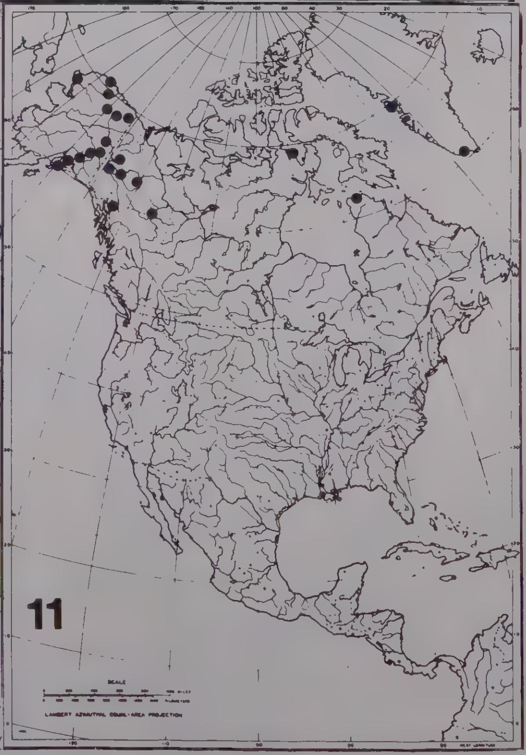


MAPS 5–8. 5. *Pohlia cruda*. 6. *Pohlia oerstediana*. 7. *Pohlia bolanderi* var. *bolanderi* (solid circles) and var. *seriata* (hollow circles). Half black circles on Mt. Rainier, Washington marks an area of sympatry. 8. *Pohlia longicollis*.

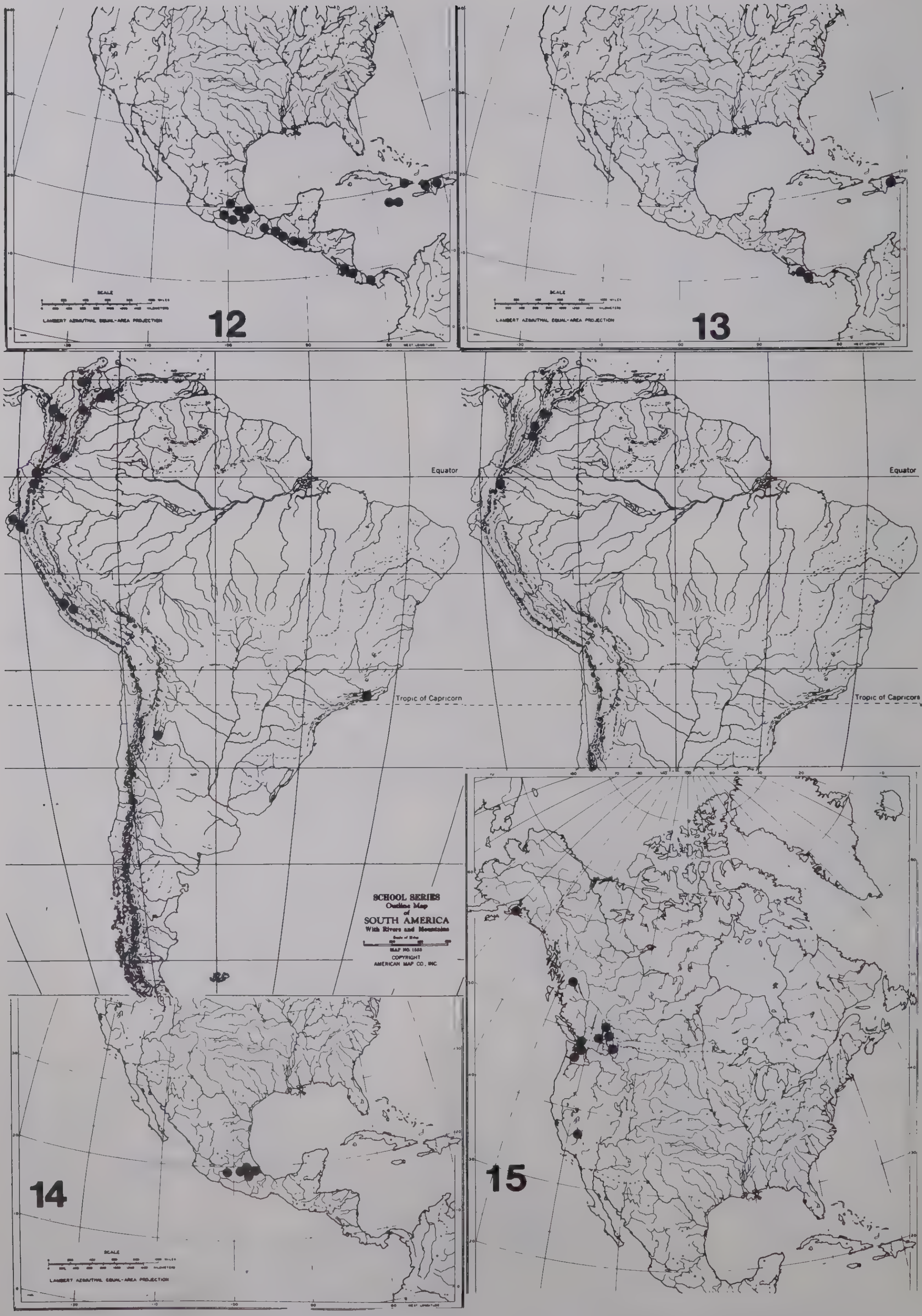




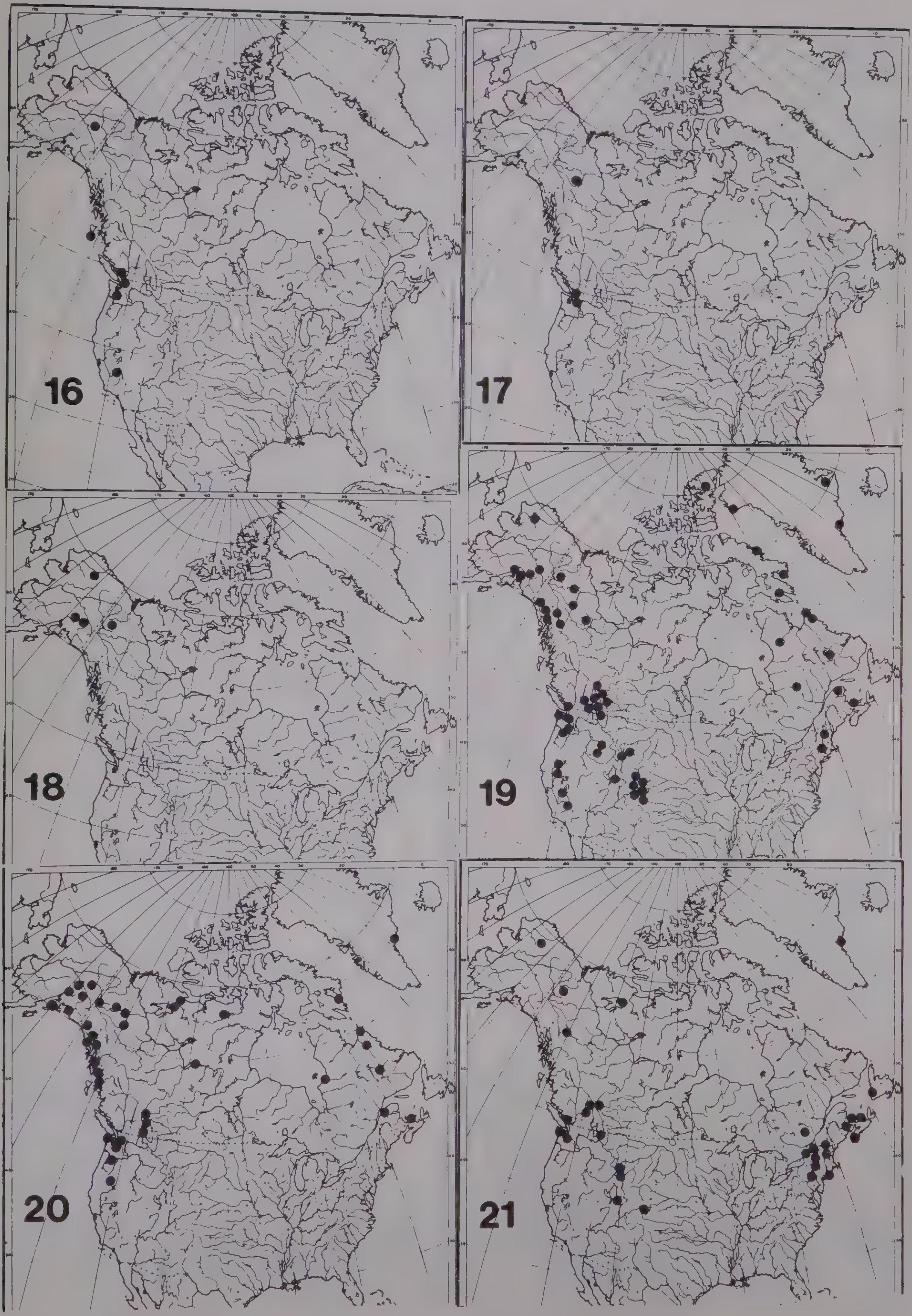




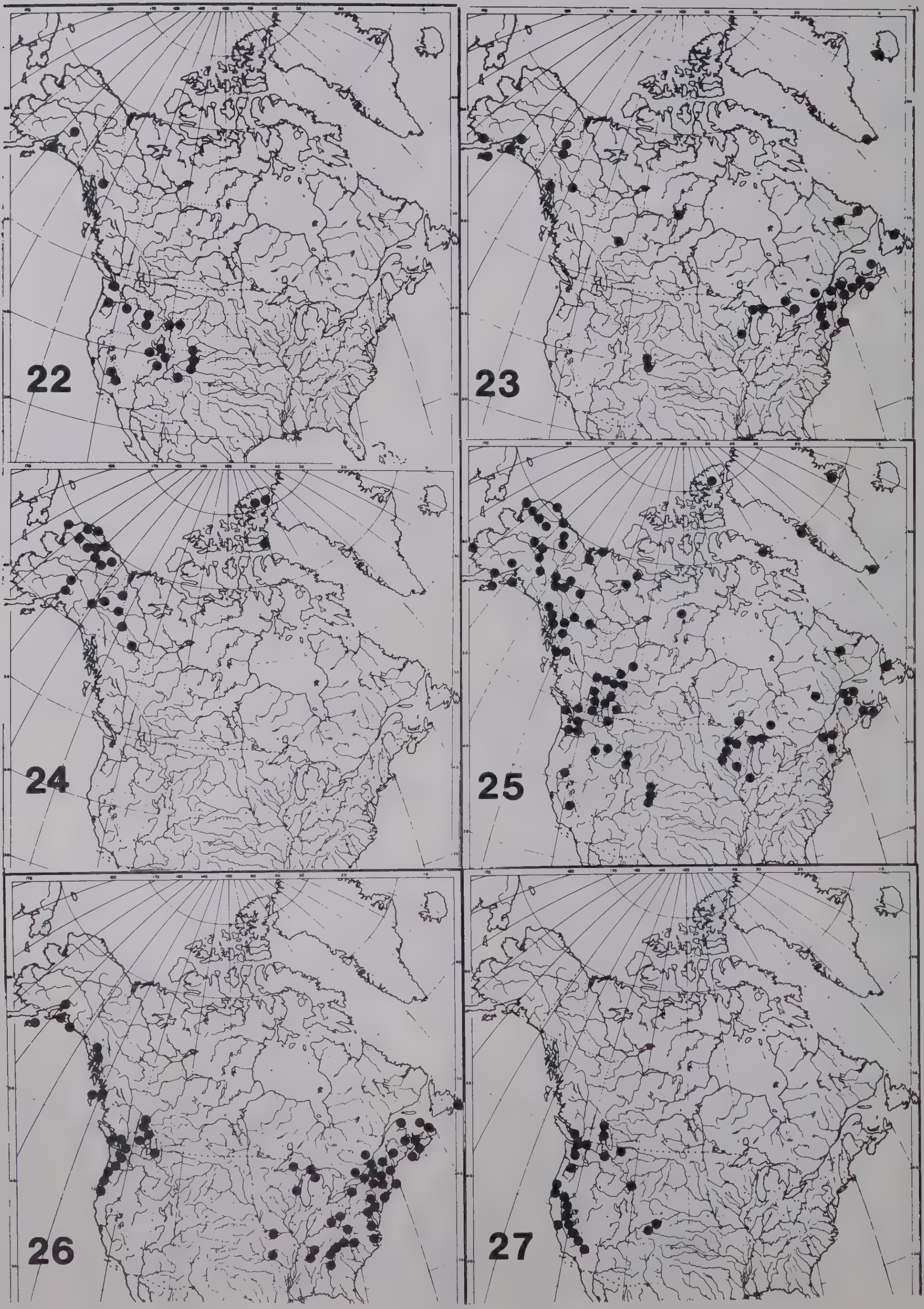
MAPS 9–11. 9. *Pohlia polycarpa*. 10. *Pohlia obtusifolia*. 11. *Pohlia crudoides*.



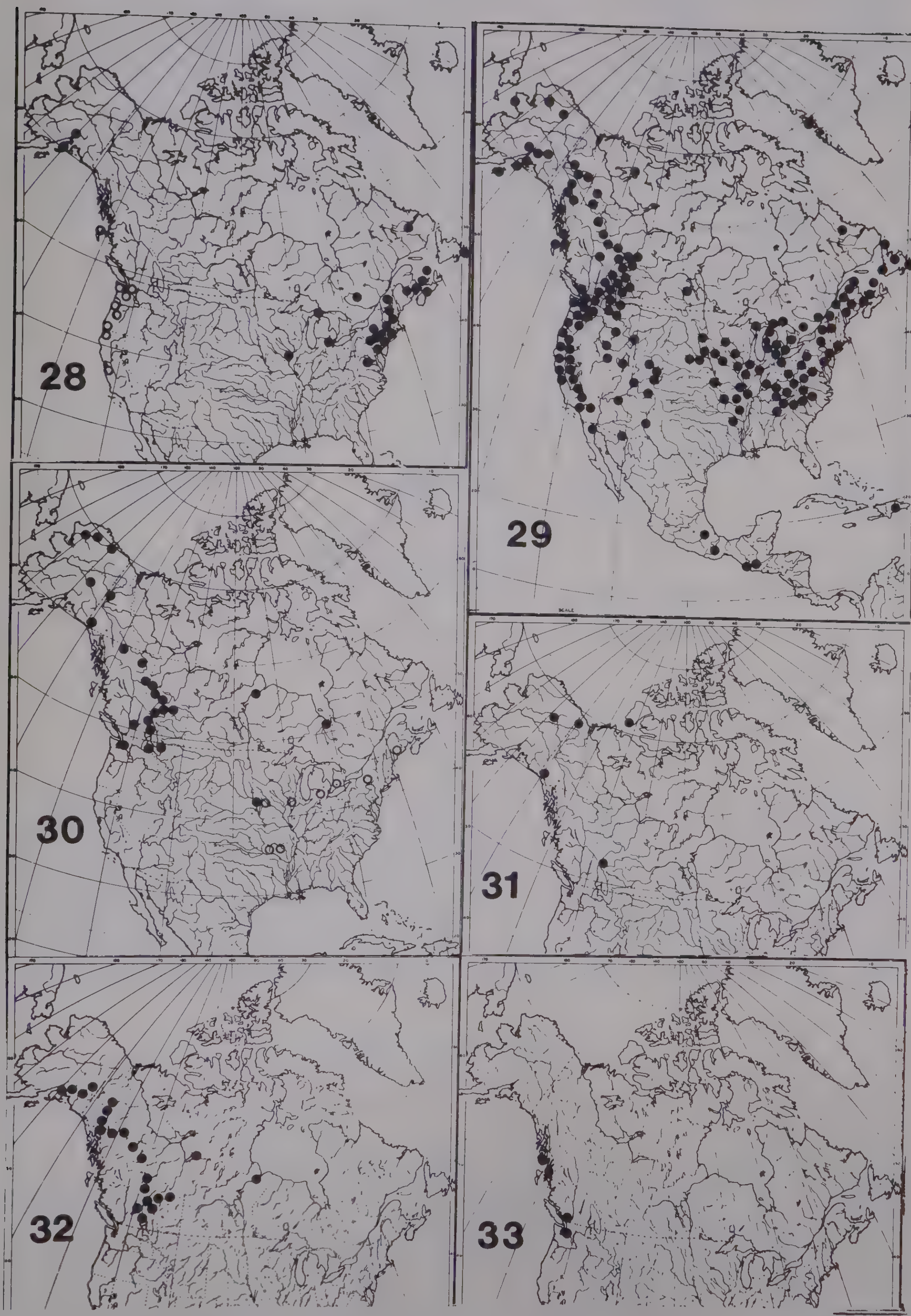
MAPS 12–15. 12. *Pohlia papillosa*. 13. *Pohlia richardsii*. 14. *Pohlia pseudo-barbula*. 15. *Pohlia ludwigii*.



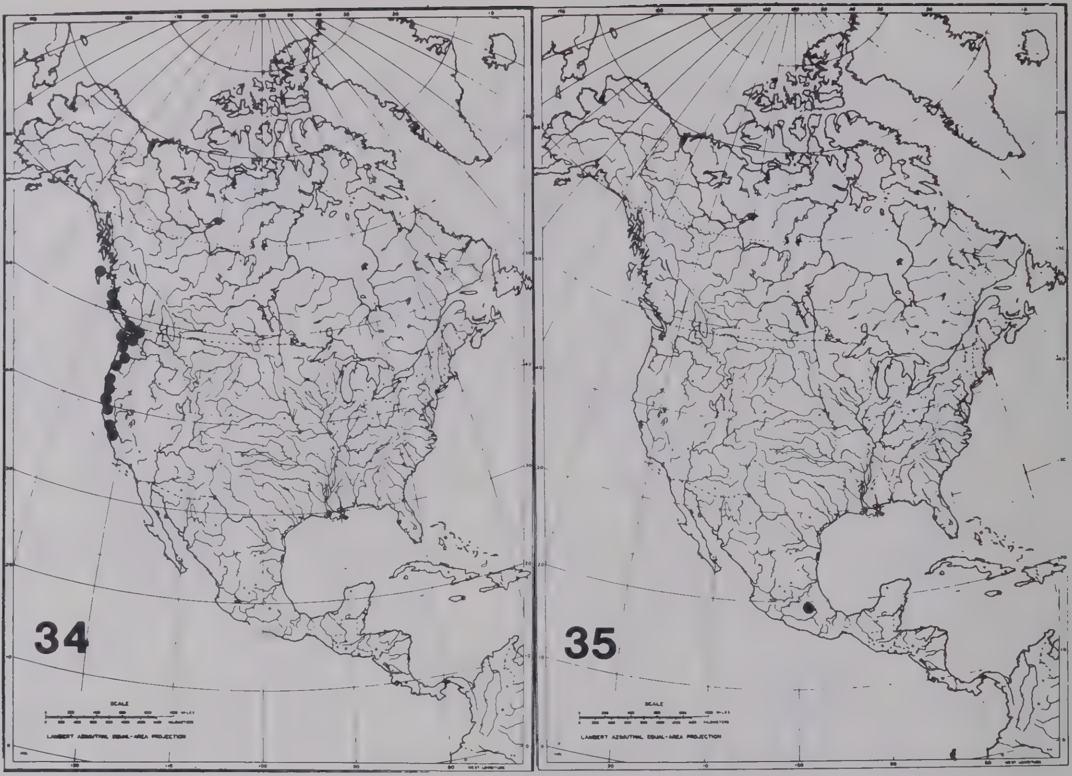
MAPS 16–21. 16. *Pohlia cardotii*. 17. *Pohlia erecta*. 18. *Pohlia beringiensis*. 19. *Pohlia drummondii*. 20. *Pohlia filum*. 21. *Pohlia andalusica*.



MAPS 22–27. 22. *Pohlia tundrae*. 23. *Pohlia bulbifera*. 24. *Pohlia andrewsii*. 25. *Pohlia proligera*. 26. *Pohlia annotina*. 27. *Pohlia camptotrachela*.



MAPS 28–33. 28. *Pohlia pacifica* (hollow circles) and *Pohlia lescuriana* (solid circles). 29. *Pohlia wahlenbergii* 30. *Pohlia atropurpurea* (solid circles) and *Pohlia melanodon* (hollow circles). 31. *Pohlia brevinervis*. 32. *Pohlia vexans*. 33. *Pohlia columbica*.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MAPS 34–35. 34. *Pohlia longibracteata*. 35. *Pohlia integra*.

ACKNOWLEDGMENTS

H. Crum was a constant and invaluable source of inspiration and advice throughout this study. His time and interest is much appreciated. I am indebted to D. Vitt, who first suggested a study of *Pohlia*, and who guided me through early stages of the research. Curators too numerous to name made this revision possible by arranging loans of specimens. D. Ernet of the Landesmuseum Joanneum Graz, took considerable time to prepare labels and arrange a loan of type material for *P. proligera*. It was through my oversight that I neglected to thank him in a previous paper. This research was supported by grants from the Boreal Institute for Northern Studies, Edmonton, Alberta, with partial support from an NSF grant to William R. Buck and an NRC grant to D. Vitt.

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